DOES CONSIDERATION OF THE WIND FIELD IMPROVE PREDICTIONS OF ZOOPLANKTON ABUNDANCE IN HARP LAKE, ONTARIO?

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Abstract

The predictability of zooplankton abundance under wind-driven currents has rarely been explored and further study can help improve the understanding of zooplankton communities in aquatic ecosystems. In this study, we sought relationships between the wind field and fortnightly abundances of 8 zooplankton species at a mid-lake station in Harp Lake, Ontario from 1980 to 2004. Over the study period, average wind speed has declined by 25%, while direction has shifted 21 degrees towards the north. Multiple linear regressions were generated to predict seasonal and interannual changes in daily zooplankton abundance combining year, Julian day, chemistry and, finally, wind speed and direction. The wind field was successfully loaded into these models for 6 of the 8 species, although improvements in predictive power were modest. We suspect that the decrease in wind speed has contributed to a change in zooplankton heterogeneity in the lake, and thus a change in bias of lake-wide abundance estimates derived from a single station. Zooplankton are patchily distributed, but most long-term monitoring programs sample only at one station. Our work suggests that we may well be able to correct for any bias emanating from a changing wind field and improve the predictability of abundance.

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General Introduction

Limnologists have been interested in the effects of wind on the physics and biology of lakes for a century now. Taylor (1916) was among the first physicists to examine the effect of wind on the Earth`s surface, and to attempt to quantify and measure wind as a consequence of friction velocity at a surface, i.e., to think of wind as a phenomenon of boundary layer physics. Early researchers were occupied with methods of interpretation and graphical representation of wind data (speed and direction) (Meisinger 1921; Crutcher 1956) as well as the mechanics that produce the wind force on an object (Van Bemmelen 1920; Langmuir 1938; Brooks et al. 1946; Durst 1948; Francis 1951). Currently, the research on effects of wind on aquatic ecosystems is vast, but the classic focus of wind effects on physics and ecology remains, e.g., including studies on the wind-induced transfer of oxygen into water bodies (Ro et al. 2007), and those examining how wind-induced mixing affects predator-prey contact rates and thus the feeding rates of larval capelin on zooplankton (Frank and Leggett 1982).

Various annual scales must be used when examining the effect of wind on a body of water. Annually averaged wind data can give an overview of how long-term changes in local climate and surface roughness of landscapes can alter wind effect from one year to the next. Such long-term changes in annual averages may also be appropriate for examining wind effects in large basins, such as the ocean where the circulation time frame is longer given the fetch length (Deser et al. 1999). However, in smaller basins daily or hourly wind data are needed to capture the detailed relationships between the wind-induced mixing of planktonic animals, and their place (depth and location) in the

water. For example, Waife and Frid (1996) used hourly wind data to examine the horizontal structure of zooplankton communities during periods of high turbulent mixing in the coastal waters off Northumberland, England. Hourly wind data needed to be used because the full tidal cycle in these coastal waters was 12.5 hours; therefore annual hourly data would not be useful (Waife and Frid 1996). Using multiple linear regression models, they discovered that 52% of the variation in the horizontal patchiness of the zooplankton community could be attributed to the wind field, even though the individual zooplankton were able to hold their horizontal position for 3 consecutive hours under any type of mixing. Therefore, depending on the question posed and the system studied, both annual or daily wind data may be needed to link biotic distributions in lakes to environmental wind forcing.

Recent advances in instrumentation and the dynamic modelling of water movements (Blukacz et al. 2009) in complex basins, have led to a growing popularity of wind research. In aquatic ecosystems, zooplankton are the common target for such studies, because they are organisms that are susceptible to wind effects (Owen 1989; Caceres and Soluk 2002). Since winds induce currents that dampen with depth in the mixed layer, zooplankton distributions are affected. Zooplankton are small pelagic animals that are easily sampled, and are found in non-random distributions in vertical and horizontal dimensions of lakes and oceans (Dirnerger and Therlkeld 1986; Waife and Frid 1996). For instance, Owen (1989) determined that microplankton in the open waters off southern California and northern Peru were more patchy at low wind speeds, and less

patchy (more homogeneous) at higher wind speeds (Owen 1989). In fact, wind events only a few hours long drove these distributions (Owen 1989).

While many studies have concluded that wind does have an effect on zooplankton distributions via wind-induced mixing of water columns (Heaps and Ramsbottom 1966; George and Edwards 1976; Thackeray et al. 2004; Rinke et al. 2007), we have much to learn about the details. How great is the effect of wind on the distribution of zooplankton? Can this wind effect be quantified over both short and long-terms, e.g., how much of the variation in zooplankton distribution does it explain? Can the predictability of either zooplankton distribution, or the long-term changes in zooplankton abundances in lakes be improved by inclusion of wind metrics in models? My purpose is to answer these questions.

Here, I address these questions in Harp Lake, a small dimictic lake that has been the focus of long-term ecological research and monitoring by personnel of the Ontario Ministry of the Environment's Dorset Environmental Science Centre (DESC) (Yan and Strus 1980; Yan and Pawson 1997; Paterson et al. 2008; Yan et al. 2008; Young et al. 2009). Zooplankton are collected biweekly from Harp Lake at a single permanent station at the deepest point of the lake (Yan et al. 2008). The physics, chemistry, and biology of Harp Lake have changed over the last 3 decades. It is warmer in the fall than it once was (Palmer et al. in revision). It has experienced long-term decreases in Ca, total phosphorus, and SO_4 as well as increases in pH and NaCl (Yan and Pawson 1997), and these chemical and physical changes correlate with long-term changes in the zooplankton community at annual steps (Yan et al. 2008; Rusak et al. 2008). In 1993, Harp Lake was

also invaded by a nonindigenous zooplanktivore, *Bythotrephes*, which has reduced the richness and affected the structure of the lake's zooplankton community, while its consumption has reduced or even eliminated several zooplankton species despite their high production (Yan and Pawson 1997; Dumitru et al. 2001; Yan et al. 2002). At this point, no one has yet considered the possibility that the wind field over the lake has changed and that this potential change may explain some of the variability in zooplankton abundance.

In Chapter 1, I examine the long-term trends in zooplankton abundance in Harp Lake and the wind field (speed and direction) between 1980-2004 at annual steps. I began with annual steps because this is the time frame over which much of the published Harp Lake work has been evaluated (e.g., Yan et al. 2001; Yan et al. 2008), and there appears to have been long-term changes in wind field at annual steps. Therefore it seemed a logical starting time frame for my work. Chapter 1 first demonstrates that wind speed and direction have changed over the last 3 decades in the region. This change raises the possibility that zooplankton spatial distribution may have changed in the lake as well, and that long-term estimates of zooplankton abundances assessed at a single mid-lake station may have biased results that reflect the long-term changes in the wind. I examined relationships between residuals of annual abundance and wind data after first modelling the variability that could be attributed to various annual predictors (considering simply the presence/absence (P/A) of *Bythotrephes*, the average surface temperature and the growing season duration, as days since ice breakup in the spring). The variability in abundance that was attributable to *Bythotrephes* P/A was expected to

be large over the study period because *Bythotrephes* appeared mid-way through this period (mid-1990's) (Yan and Pawson 1997). I found that five of the eight species had abundance that could be significantly explained by *Bythotrephes* P/A in regression models. I also confirmed that the wind field over the region was significantly changing, where speed was found to be decreasing and direction shifting more towards the north. Despite the changing wind field, the prediction of the annual mean of zooplankton abundance could not be improved by considering wind speed or direction for seven of the eight species.

In Chapter 2, I examined the influence of changes in the wind on daily abundances of zooplankton in Harp Lake between 1980-2004, to discern if abundance of various species can be better predicted when considering the effect of wind in addition to temporal and chemical predictors. For this purpose, I used multiple linear regression models to predict the abundance of the zooplankton species, first using temporal and chemical predictors. All zooplankton species had abundance that could be explained by year/day of year alone. Six of the 8 zooplankton species had abundance that could be better predicted by the inclusion of wind in the multiple linear regression models, in addition to year/day of year and water chemistry. All metalimnetic species in this study had abundances that could be better explained by the inclusion of a wind metric. The wind field could not predict smaller, slow zooplankton species in the multiple linear regression models.

My study comes at an important time in the progression of wind research. We now have 3-D, finite element water mass movement models (Blukacz et al. 2009), the

capacity to measure plankton biomass in continuous transects with laser optical plankton counters (Behrenfeld and Boss 2006), and hydroacoustics (Rinke et al. 2007), but can we include wind to help in the interpretation of long-term planktonic datasets? (whose use for management purposes is of late being questioned) (Allen et al. 1999; Jeppesen et al. 2011). Of the many wind-plankton studies since Taylor (1916), there has not been a study that examined 25 years of changes in zooplankton abundance, water chemistry variables and wind at both annual and daily time frames.

In addition to searching for a predictive relationship between zooplankton abundance and the wind field, I also hope to promote zooplankton as a model community for bioassessment. Bioassessment programs rarely include zooplankton among their biological indicators because too much of the variability in zooplankton metrics is unexplained (Allen et al 1999). It is quite possible that zooplankton sampling procedures were poor, i.e. they did not adequately capture the patchiness known to occur, and to influence abundance and composition estimates (MacKenzie and Leggett 1991; Roemmich and McGowan 1995; Waife and Frid 1996). By acknowledging that wind affects zooplankton spatial distributions, and must be accommodated by sampling procedures for accurate and precise abundance estimates, future biomonitoring by scientists may well discover that zooplankton do provide information that can be strongly related to anthropogenic stressors (O'Connor et al. 2000).

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Chapter 1:
The wind field does not improve predictions of annual average zooplankton abundance in Harp Lake, Ontario

Abstract

Zooplankton ecologists have generated a large number of multi-decade, mid-lake, zooplankton datasets, but the long-term dynamics of zooplankton heterogeneity induced by wind-driven currents has never been explored. If wind speed or direction changes over time, then the distribution of animals may also change, and abundance assessed at a single station may have changed with the wind field. In this study, I determine if changes in the annual averages of the abundance of 4 Cladoceran, 2 Calanoid and 2 Cyclopoid species in Harp Lake, Ontario, were related to the wind field (speed and direction) between 1980 and 2004. Zooplankton data were generated from a volume-weighted composite of multiple vertical hauls taken from a single station at the deepest point of the lake. Wind speed has decreased, on average by 25%, while wind direction has shifted by 21 degrees towards the north. In order to assess if the variation in abundance was influenced by this change in the wind field, I first needed to correct for the other known long-term changes in lake's zooplankton. Hence, to consider how annual climatic differences might have influenced the community, I began by regressing zooplankton abundance against the presence/absence of *Bythotrephes*, the average number of days since spring ice break-up, and the average surface temperature on sampling days. I then determined if the residual variation in average zooplankton abundance from these models was correlated with the wind. Despite long-term changes in the wind field, linear-linear (speed) and linear-circular (direction) correlations of annual residual abundance of 7 of

the 8 species were not predictable from the wind fields using the averages of the sample day. The exception was *D. mendotae*, for which residual abundance was correlated with wind direction (r^2=0.2300, p=0.005) meaning that the high residual abundance was correlated with a particular wind direction. *D. mendotae* is a large, fast swimming cladoceran that may be predictably responding under turbulent mixing and the resulting thermocline tilting in the hypolimnion. In summary, on an annual basis, long-term changes in zooplankton abundance were not improved by changes in the wind field.

Introduction

Because of predictable responses to anthropogenic stressors, zooplankton have been used to document both the damage caused by, and subsequent recovery from various pollutants, such as acid rain (Marmorek and Korman 1993; Arnott *et al.* 2001). However, failure to consider spatial dynamics may reduce the usefulness of zooplankton as bioindicators of damage and recovery (MacKenzie and Leggett 1991). The distribution of zooplankton varies vertically and horizontally in lakes, and this distribution should be understood if we are to use them as indicators. The horizontal distribution of zooplankton is influenced by predation by littoral fish (Glizicz and Rykowska 1992), and wind-induced currents (Burkes et al. 2002). The diel vertical distribution of many species changes in response to a warming climate (Pinel-Alloul 1995; Lampert et al. 2003; Semyalo et al. 2009), to predation pressure from macroinvertebrates (Young and Yan 2008), fish (Dodson et al. 1997; Larsson and Lampert 2011), and to UV radiation (Lampert 1989; Leech and Williamson 2001).

Hence, to understand the impacts of both natural and anthropogenic drivers on zooplankton we need to understand the determinants of their spatial heterogeneity.

In comparison with other biota, the correlations of zooplankton community structure with many environmental stressors (e.g., shoreline disturbance, altered water chemistry, riparian disturbance, littoral macrophyte coverage and human development) are relatively weak (Allen et al. 1999; O'Connor et al. 2000). Thus, zooplankton have not been routinely recommended for inclusion in large scale, bioassessment programs (Jeppesen et al. 2011). However, the majority of zooplankton sampling procedures would not capture the patchiness or heterogeneous distributions known to occur (Folt and Burns 1999; Pinel-Alloul and Ghadouani 2007). Typical zooplankton monitoring programs use short-term studies with few sampling stations (Allen et al. 1999). Thus accurate zooplankton community distributions are unlikely. Patchiness is indeed the normal expectation (Folt and Burns 1999). For example, Malone and McQueen (1983) found that horizontal distributions of zooplankton were patchy even in small, single-basin lakes (Pinel-Alloul and Ghadouani 2007). Yan and Strus (1980) found that this patchiness could commonly include the standing stock of the entire community, not just individual species. Thus, we should not be surprised by low correlations of zooplankton assemblage structure with environmental factors in 186 northeastern United States lakes when sampling involved a single mid-lake station (Allen et al. 1999). As patchiness may contribute a large portion of the unexplained variance in large-scale assessments, it may be too soon to conclude that correlations of zooplankton community structure with environmental drivers are weaker than similar relationships for other groups of biota.

The risks of ignoring zooplankton patchiness in studies of zooplankton dynamics are understood (Prepas and Rigler 1978), but still usually ignored.

The body size, swimming ability and diel vertical migration of zooplankton influence how they are re-distributed by wind-driven currents in lakes (Dirnerger and Threlkeld 1986; Zurek and Bucka 2004). The swimming speed of cyclopoids increases with body size (Saunders and Lewis 1988); therefore, large animals should be able to maintain their position in currents better than smaller conspecifics. It is expected that organisms inhabiting the surface waters of lakes will be more affected by wind-induced currents than those organisms found in the meta- and hypolimnion (Naithani et al. 2003). Zooplankton that are strong swimmers, such as *Leptodiaptomus minutus* (0.340 cm/s, Muirhead and Sprules 2003) can swim against and out of turbulent layers of the water and remain in a specific location (Woodson et al. 2005). Epilimnetic zooplankton require greater swimming abilities to maintain their position in the more turbulent surface layers. Those zooplankton found in deeper waters inhabit denser and less turbulent water than epilimnetic species, and therefore, require less effort to maintain their position in the water column (Woodson et al. 2005). Therefore, we need to understand wind-driven water movements and density gradients in lakes as well as the behaviour and swimming abilities of zooplankton to understand the distribution of animals. It starts with the wind.

What generates wind? Wind is the product of Newton's Second Law of Motion (force = mass*acceleration) and the friction between air masses and surfaces (Ahrens 2000). When a low-pressure air mass (generally warm air) comes in contact with a high-pressure air mass (generally cooler air), an intervening pressure gradient is generated

(Ahrens 2000). A high-pressure air mass will always move towards a low-pressure air mass (Butz 2004). Newton's 2nd law implies that the acceleration and change in pressure within the pressure gradient causes force on an object, e.g., wind is the result of the forces operating between air masses with different pressures (Ahrens 2000). The pressure gradient determines the strength of the wind, e.g., its speed, moving over a surface (Ahrens 2000).

Wind speeds at surfaces are influenced by the roughness of that surface. Optimal laminar flow is consistent with smoothly gliding air masses over a smooth, stationary medium (Ahrens 2007). Surface roughness caused by trees and buildings increases eddy viscosity, which then generates friction among eddies and an irregular production of whirling winds (Ahrens 2007). For example, Tanentzap et al. (2007) found a 34% decrease in annual average wind speeds at Sudbury Airport over the preceding 3 decades attributing this to an increase in surface roughness, caused by forest growth in a previously barren, industrial landscape. It is important to note that the airflow over rough land versus smooth water has a dramatic effect on wind dynamics (Ahrens 2007). Since water is smoother than land, there is less friction and therefore wind speeds are faster over large water bodies compared to adjacent, normally "rougher" land (Ahrens 2007). Aside from wind speed, wind direction itself can have interesting effects on the climate and weather systems surrounding bodies of water. Changes in wind direction can cause changes in the climate especially since lakes are not commonly circular. The direction of wind can bring in cooler air masses to a particular area and cause storms and windy behaviour.

The interplay of wind dynamics with water masses, and the swimming ability and diel behaviour of zooplankton all influence zooplankton distribution. The topography and cover of the watershed and the shape and size of the lake basin influence water movement within the lake (Ahrens 2007). Winds mix and move water masses thus altering the distribution of zooplankton populations in the water column (George and Edwards 1976; Cloern et al. 1992; Naithani et al. 2003; Vanschoenwinkel et al. 2008). Wind-induced currents begin in the epilimnion where water is pushed downwind, the direction away from the origin of the blowing wind (Zurek and Bucka 2004) (Figure 1.1). Plankton that prefer epilimnetic waters will be concentrated downwind if they are able to swim faster than the speed of the downwelling water at the downwind end of the lake. If animals are not able to swim faster than the downwelling current, they will be moved, conveyor-like, downward with the downwelling current, then upwind with the deeper water return current (George 1981, Blukacz et al. 2009). In this case, animals will be concentrated into lower strata (Naithani et al. 2003). In contrast, plankton that prefer lower strata (e.g., metalimnion or hypolimnion) are upwelled by internal waves (seiches) and may become concentrated upwind in warmer surface waters (Naithani et al. 2003). Of course, wind speed and direction change frequently, thus actual distributions of animals are a product of recent wind forcing, and a legacy of preceding wind fields, where the influence of past winds decreases with year.

Changes in zooplankton distribution that are induced by changes in the wind may confound our ability to detect the influence of many drivers on zooplankton abundance, especially if we sample at only one site. Few studies have explored the long-term noise

that can be generated from wind-induced currents and the impact it may have on their results (Owens 1989; Blukacz et al. 2009; Mackenzie and Leggett 1991). For example, Mackenzie and Legget (1991) found that weak wind-induced currents caused zooplankton to be patchily distributed on a vertical scale of 5-10 m. Although they focused on tracking predator-prey contact rates, that study provides an example of how the wind may affect zooplankton distributions.

Here, I focus on Harp Lake, a small (71.4 ha), single-basin, Canadian Shield lake that has been monitored by personnel of the Ontario Ministry of the Environment's (MOE's) Dorset Environmental Science Centre (DESC) for over 30 years (Yan and Strus 1980; Yan and Pawson 1997; Paterson et al. 2008; Yan et al. 2008; Young et al. 2009). Zooplankton are collected from Harp Lake at a single permanent station at the deepest portion of the lake (Yan et al. 2008). Harp Lake is changing in many ways. NaCl levels are increasing because of the maintenance of winter roads (Molot and Dillon 2008), and DOC levels are increasing likely because of slight reductions in acidity (Monteith et al. 2007), and climatic changes (Keller et al. 2008). Phosphorus and Ca levels are declining (Yan et al. 2008).

In the early 1990s, Harp Lake was invaded by a nonindigenous zooplanktivore, *Bythotrephes longimanus*, which has reduced zooplankton richness and affected the structure of the zooplankton community (Yan et al. 2002). Dumitru et al. (2001) found that *Bythotrephes* consumption has reduced or eliminated several zooplankton species despite their high production (Yan and Pawson 1997). Zooplankton species that remain in Harp Lake are those that are too large for *Bythotrephes* to consume (e.g., *Holopedium*),

too fast for *Bythotrephes* to catch (e.g., *Daphnia mendotae*) (Dumitru et al. 2001), or reside in layers *Bythotrephes* does not frequent (e.g. *L. sicilis*). Petruniak (2009) found that *Bythotrephes* had an aggregated spatial distribution in Harp Lake in 2007, both across the whole lake and in the region of the lake outflow, and her model runs suggested there were predictable changes in the horizontal position of *Bythotrephes* in the lake from day to night. Therefore, Harp Lake is ideal for my study because the native zooplankton species may exhibit the same wind-induced patterns that have been observed for *Bythotrephes.*

I also chose Harp Lake because of its sampling frequency (fortnightly in all years, Yan et al. 2008), its predator-simplified zooplankton assemblage, its probable lack of water quality or habitat control of its zooplankton assemblage, its well oxygenated hypolimnion (unlike several of the other dimictic lakes), the fact that it never acidified, that Ca^{2+} levels were always above damaging thresholds (Ashforth and Yan 2008), that it had a strong mid-record signal from the invasion of *Bythotrephes,* and, because the vertical distribution of zooplankton in the lake had been assessed. Studies of zooplankton species in temperate lakes like Harp Lake (e.g., *D. mendotae*) have found that animals migrate to different water depths, depending on factors such as predator presence and food availability (Pinel-Alloul 1995; Folt and Burns 1999). Young and Yan (2008) discovered that *Daphnia*, *Bosmina*, and copepod populations migrated vertically at night in Harp Lake. In particular, *Daphnia mendotae* occupied the epilimnion during the night and migrated to the hypolimnion during the day (Young and Yan 2008).

Despite research on the influence of wind on zooplankton distributions, no one has determined if long-term changes in the wind contribute to the variability in zooplankton abundance. Such a study would be justified because wind speed does have a significant effect on estimates of zooplankton biomass (Frank and Leggett 1982), and also alters zooplankton distributions. Here my overall goal was to examine the long-term trends of zooplankton abundance in Harp Lake, and to determine if these trends are correlated with changes in the wind field (speed and direction) examined at annual steps. My objectives were: (1) to determine if there were significant long-term trends in the regional wind field from 1980-2004, (2) to extract the annual residuals of zooplankton abundance from regression models based on *Bythotrephes* P/A, average surface temperature, and days since spring ice break-up, and (3) to examine the correlation between the residual abundance from these models and the regional wind field patterns.

I predict that zooplankton species inhabiting the surface waters are affected by wind-induced currents, that the residual abundance of epilimnetic species will not correlate with the wind field, because their distribution in the surface waters will be homogenized by the wind. Those species typically found in the lower depth strata will be less affected by the wind field, and will be able to hold their position in the water column at lower wind speeds. As wind speeds fall to a point where these animals can resist advection by wind-induced currents, they will become more patchy as well as being able to hold their position in the water column. Thus residual abundance will increase for these species as wind speed falls. For example, Visser et al. (2009) found that large, strong swimming copepods could hold their position in the water despite the turbulent

mixing. The relatively high swimming speed of copepods versus cladocerans is well documented, thus copepods are expected to withstand the wind-induced current (Link 1996; Woodson et al. 2005; Visser et al. 2009). Smaller and slower zooplankton species will be easily re-distributed in the water column and will not exhibit any predictable changes in residual abundance. In other words, any reduction in wind speeds should not be enough to let patches form and thus allow a change in the distributional patterns that would lead to a correlation with the residual abundance and the wind. Larger and quicker zooplankton species will not be so easily re-distributed in the water column and will be able to maintain their distribution pattern.

Methods

Harp Lake (45°23'N, 79°07'W) is a small (71.4 ha), stratified, dimictic lake with a maximum depth of 37.5 m (Paterson et al. 2008; Young et al. 2009) (Figure 1.2). It is one of 8 Canadian Shield lakes in south-central Ontario that has been the subject of long-term biological and chemical monitoring by the Ontario Ministry of the Environment's Dorset Environmental Science Centre (DESC) (e.g., Yan and Strus 1980; Yan et al. 2008). Crustacean zooplankton are collected biweekly in vertical net tows (from 6, 6, 13, 21 and 30m to the surface) at the deepest portion of lake during the ice-free season using a conical zooplankton net with a length of 138.43 cm, a diameter of 12.4 cm, and a mesh size of 76 um (Girard et al. 2007). Sample volumes are calculated from net haul lengths and the measured net filtration efficiency (Girard et al. 2007).

Over the last 30 years, many limnological changes have been documented in south-central, Ontario lakes, and Harp Lake is no exception. It has experienced increased concentrations of Na, Cl, Mg and dissolved organic carbon (DOC) and decreases in pH, Ca and total phosphorus (TP), for reasons discussed by Paterson et al. (2008), Molot and Dillon (2008), and Yan et al. (2008). In the early 1990s, Harp Lake was invaded by a predatory Eurasian cladoceran species, *Bythotrephes longimanus*, which has reduced zooplankton species richness and affected the zooplankton community structure of the lake (Yan et al. 2002). Yan and Pawson (1997) found that prior to the invasion of *Bythotrephes* in 1993, the total biomass and diversity of the zooplankton community was relatively stable. After the invasion, two larger cladocerans (*D. mendotae* and *H. glacialis*) became more abundant while many species declined or completely disappeared including *D. birgei*, *B. tubicen* and *T. extensus* (Yan and Pawson 1997).

I used zooplankton data from 1980-2004 for my study. Yan et al. (2008) have reported the general changes in the composition, body size and species richness of the zooplankton community of the lake over this study period, but have not considered possible effects of the wind field on the lake zooplankton. N. D. Yan provided me with the raw zooplankton data.

Bythotrephes in Harp Lake have been found to respond to the wind field (Petruniak 2009), and I saw no reason why other zooplankton should not also respond. In addition, given the fortnightly sampling for multiple decades, the abundance of data was vast. Zooplankton characteristics that might influence their vulnerability to the wind, excluding abundance and body size (which came from the Harp Lake data) were

identified from a review of literature. I selected species for this study based on their body size, their swimming ability, pelagic habitat, and their frequency of occurrence in the database (common and abundant taxa). I modelled the relationship between annual zooplankton abundance and *Bythotrephes* P/A, the average surface temperature, and average number of days of sampling since ice off, then determined if there were any significant correlations between the residual variation in abundance and the wind field. As independent variables I first used *Bythotrephes* P/A to control for the long-term effects of the *Bythotrephes* invasion. As the first correction of the temporal sequence for interannual differences in heating season, I used Days since ice-free, e.g., the average number of days since spring ice break of all the sample dates in the year. This measure was used to explain changes in zooplankton abundance that may be due to the length of the ice-free season. Finally, I used the rate of surface heating to control for any changes the surface and bottom water temperatures (average surface temperature). These models were run using simple multiple linear regression, and then I examined the correlation of their residuals with the wind field (speed and direction, separately). Volumetric abundances of zooplankton species were available from 291 dates from 1980 to 2004 in Harp Lake. Missing values, indicating that animals were not detected in the count, were replaced with zeroes. Abundance values of the species were sorted by date, averaged by year, and compiled into tables along with the additional heating season and *Bythotrephes* P/A variables (Yan et al. 2008). I expected that *Byhtotrephes* P/A would account for previously observed changes in abundances of several species associated with the arrival of this invader in 1993 (Yan et al. 2008; Young et al. 2009). My second predictor

variable, “Days since ice-free date” was designed to reflect the fact that the date of spring ice-breakup varies substantially among years. I took ice break-up dates from the MOE, calculated the days of ice break-up from that date to each sampling date, and the average of these differences between sampling and ice break-up up formed my second annual integrator – average number of days since ice break-up. Then I took the average of all these values for each year as my average days since ice break-up. My average surface temperature variable was a measure of the water temperatures in the surface waters in each year, as changes that occur in the heating of the surface waters over the study period may affect abundance. In other words, the annual average surface temperature using the heating rates over baselines of the hypolimnion on the days of sampling. To calculate the average surface temperature (AST) metric I used the water temperature at 1 m depth from the surface and took the average of all those measured values for the year. Days since ice-free and the average surface temperature were used in addition to *Bythotrephes* P/A to better explain the variation in abundance that may be attributable to a potentially warming climate (denoted by longer ice-free seasons or warmer the surface water heating with year)

The following zooplankton species were used (Table 1.1): *Daphnia mendotae, Holopedium glacialis (*formerly *Holopedium gibberum*), *Bosmina tubicen, Diaphanosoma birgei, Leptodiaptomus sicilis, Leptodiaptomus minutus, Diacyclops bicuspidatus thomasi* and *Tropocyclops extensus (*formerly *Tropocyclops prasinus mexicanus)* based mainly on their frequency of occurrence in the database, but also to provide a range of swimming speed, body size, order/class and preferred temperature

stratum. Abundance and body size were taken from the MOE's Harp Lake data. A literature search was done using ISI's Web of Science using the keywords: zooplankton, distribut*, body size, swim* speed, diel migrat*, feed*, vertical depth and the scientific names of each zooplankton species. This search provided the information needed to compile the physical and behavioural characteristics of the selected species.

As dependent variables for each species, I considered: abundance, LOGabundance, SQRTabundance. The later two variables were used to transform the averaged abundance data and the use of one instead of the other depended on the residuals that resulted from these regression models. As independent variables, I considered the dummy variable *Bythtrophes* P/A (Bytho), Days since ice-break (or the average Julian date since ice-free of all the samples in the year) (Free), the average surface temperature in Julian date at the last sample date (AST), $Free^2$, AST^2, Bytho x Free, $(Bytho \times Free)^2$, Bytho x AST, $(Bytho \times AST)^2$, Free x AST, and $(Free \times AST)^2$. All species had abundance log-transformed (LogAbundance) to reduce heterogeneity and to reduce outliers observed in regression plots.

Wind Characteristics

Wind direction (recorded in degrees) and wind speed (recorded in km/h) were taken from the online National Climate Data and Information Archives through Environment Canada (http://climate.weatheroffice.ec.gc.ca/climateData/canada_e.html) as hourly data from 1980-2004 on the zooplankton sample dates. All wind directions report the direction the wind is blowing from. The MOE's DESC maintains a

meteorological station in the Harp Lake watershed, however forest growth around the MET station has reduced the accuracy of, and introduced substantial bias to, the wind data. Therefore, I used the data from the next closest, well-maintained, meteorological recording station at the Muskoka Airport near Bracebridge, Ontario, Canada (44°58'29N, 79°18'12W, approximately 60 km from Harp Lake). The forest height around the Muskoka Airport is maintained for aircraft safety (personal communication, Mark Stirling, Manager). The nearest tree is 75 m from the anemometer. This anemometer was upgraded and moved a couple of yards in 2009, but otherwise it has not been changed or its use interrupted during the period of my study, e.g., 1980 to 2004 (personal communication, Mark Stirling, Manager, Muskoka Airport).

How does the wind speed compare between Muskoka Airport and Harp Lake?

The wind field at the Muskoka Airport may not accurately reflect the wind field over Harp Lake. I checked this in 2 ways: (1) by comparing the 2003-2004 wind speed measurements from Harp Lake and the Muskoka Airport, and (2) by comparing the wind data the DESC generates at Paint Lake, which is closer to Harp Lake, with those from the Muskoka Airport from 1990-2004. Both methods determined that Harp Lake wind speeds were much lower than Muskoka Airport and Paint Lake wind speeds. Harp Lake winds are less strong because of the forest growth over the study period.

We could not use the wind data from Harp Lake because its speeds were artefactually low compared to other wind speeds in the area and missed potentially important trends (Figure 1.3). The simplest explanation is that afforestation at the site

has swamped the anemometer, artefactually lowering wind speeds. Hence, I could not use the Harp Lake MET data. The range of wind speeds from Muskoka Airport was 0-9.734 m/s, whereas the range from Harp Lake was 0.291-3.172 m/s. The average wind speed for Muskoka Airport for 2003-2004 was 2.610 m/s, while the average was 1.210 m/s for Harp Lake. There was a significantly increasing wind speed for Muskoka Airport ($r=0.13$, $p=0.0013$) from 2003-2004 while Harp Lake wind speed did not significantly change ($r=-0.05$, $p=0.2267$).

Comparisons of data from Paint Lake and the Muskoka Airport indicate that wind speeds are fairly constant in Muskoka over the scale of tens of km. The DESC maintains a MET station at Paint Lake located 40 km from Harp Lake and 60 km from the Muskoka airport. The Paint Lake anemometer has not been absorbed by the growing forest as has happened at Harp Lake. The long-term forestation in Harp Lake may have affected the anemometer, therefore using Paint Lake, we can better prove that the wind field over Harp Lake is being obscured by the forestation. Since Paint Lake wind speeds resemble those over Muskoka Airport, we can apply the airport data to Harp Lake.

Similar to Muskoka Airport, the wind speed over Paint Lake is significantly decreasing ($r^2=0.012$, $p<0.0001$) with the same ups and downs, despite it being lower in elevation (Figure 1.4). However, the wind speed over Muskoka Airport is 1/2 the strength of the wind speed at Paint Lake (wind speed ranges: 1.87-1.45 m/s, 3.51-3.38 m/s, respectively).

Statistical Analyses

Objective 1: Has the wind field in Muskoka changed?

Because forest growth at the Harp Lake MET site has rendered its wind speed and direction data unsuitable, I employed the wind data from the Muskoka airport. I determined if the regional wind speed or direction had changed at monthly, seasonal and annual steps from 1980 to 2004. I used November to March as the winter (ice-cover) period and April to October as the ice-free period. To determine if the annual trends were significant, I employed the squared Pearson correlation of wind speed vs. year, using the Analzye-it add-on for Excel (Analyse-it Software, Ltd 2011), and linear-circular associations for wind direction, using Oriana 3.21 (Kovach Computing Services 2010). The associations provided by Oriana were given as the unsquared r-value of the Pearson correlation. If wind speed or direction was changing, then there might be some effect on zooplankton distribution in the lake, and thus some developing bias in our 1 sampling station data.

Objective 2: Does the annual trend in the wind field correlate with the changes in zooplankton abundance over Harp Lake between 1980-2004?

I calculated the residual variation in zooplankton in linear, multiple or polynomial regression models that predicted the annual average of zooplankton abundance. Then I examined the part correlations of the residuals with two components of the wind field: speed and direction. In addition to generating these residuals, I also calculated the partial correlation coefficients to explicitly determine the relationship between abundance and the wind field (speed and direction) after partialling out the effect of the various

annual steps used in the respective models for each species separately. I did this by choosing my final regression model (using the criteria below) and adding wind speed into the model and ran the new model in PAST (Hammer et al. 2010) to calculate the partial correlation coefficient for just abundance and wind speed with the other predictors in the model being partialled out. Those correlations for wind direction were not performed because Oriana 4 (Kovach Computing Services 2010) could not compute these values.

To select my final regression model I examined many regression diagnostics, i.e. correlation coefficient (r), t-statistic, and F-statistic to assess the significance of the entire model, and I examined the residuals aiming for low skewness and low kurtosis, independence, and normal distribution (Kleinbaum et al. 1988, Birkes and Dodge 1993).

Objective 3: Do the residual abundances correlate with the wind field over Harp Lake between 1980-2004?

After choosing a model to describe the long-term changes in each zooplankton species, I determined if the residual abundance might be attributable to changes in the wind field at annual steps. For all species, the abundance was non-normal (Shaprio-Wilk test, Analyse-it add-on for Excel) and I transformed the data prior to computing the residuals.

The annual residual abundances for each species obtained from the regression models were correlated with the wind field from that year using part correlations with $p=0.05$. I ran the correlations with the wind speed using Analyse-it add-on for Excel (Analyse-it Software, Ltd 2011). The correlations (r) between the residual abundance

and wind direction were performed using Oriana 3.21 (Kovach Computing Services 2010) as bivariate linear-circular associations as follows:

$$r^2 = \frac{r_{xc}^2 + r_{xs}^2 - 2r_{xc}r_{xs}r_{cs}}{1 - r_{cs}^2}$$ (Mardia 2000) Equation 1.2

where r_{xc} is the correlation between x and cos α, r_{xs} is the correlation between x and sin α, and r_{cs} is the correlation between cos α and sin α. The α denotes a circular value (wind direction) and x denotes a linear value (residual abundance) (refer to Appendix B1 for how to identify an association between residual abundance and wind direction). I compared and confirmed the part correlation coefficients generated with those calculated from the partial correlation coefficients. The part correlation coefficients were very similar or equal to those calculated using the partial method.

Results

Objective 1: Has the wind field changed in Muskoka?

On average, the wind speed has decreased from 1980 to 2004 from about 4.0 to 3.0 m/s (r^2=0.82, p<0.0001) (Figure 1.6). For the winter season, the wind speed has decreased by 0.8 m/s over 25 years from 4.0 to 3.2 m/s (r^2=0.75, p<0.0001) (Figure 1.7) and for the ice-free season, the wind speed has decreased by 1.1 m/s from 4.0 to 2.9 m/s (r^2=0.79, p<0.0001) (Figure 1.8). The monthly wind speeds from 1980-2004 decreased with the same long-term patterns as the annually averaged data (Figure 1.6, Figure 1.9ab).

On average, wind direction has shifted from 33 degrees to 12 degrees (more to the north, r^2=0.63, p<0.0001) (Figure 1.10). For the winter season, the wind direction shifted

from 35.1 degrees to 15.3 degrees (r^2=0.58, p=0.0004) (Figure 1.7). For the ice-free season, the wind direction shifted from 30.2 degrees to 8.3 degrees (r^2=0.60, p=0.0002) (Figure 1.8) The wind directions had monthly, seasonal and annual patterns that shifted more towards the north from the northeast or coming from the south/southwest (Figure 1.10, Figure 1.11ab).

Objective 2: Was the annual trend in the wind field correlated with the changes in zooplankton abundance over Harp Lake between 1980-2004?

To start, most of the zooplankton species had abundance that changed with year (Figure 1.12). The smaller species (*B. tubicen*, *D. birgei* and *T. extensus*) decreased with year beginning in 1993 while the larger species (*D. mendotae*, *H. glacialis* and *L. sicilis*) increased with year also beginning at 1993. Only 2 of the 8 species remained relatively stable throughout the study period (*L. minutus* and *D. thomasi*).

The majority of the species had abundance that was influenced by *Bythotrephes* P/A (Table 1.2). *Bythotrephes* appeared in 1993 and was found in Harp Lake for the remainder of the study (Figure 1.13). All cladoceran abundances significantly changed with the presence of *Bythotrephes*. *L. sicilis* was the only copepod that had abundance significantly affected by the presence of the invader.

The average surface temperature influenced zooplankton abundance (Figure 1.14). In fact, the average surface temperature varied by almost two fold between years from 10.82 to 18.33 degrees (Figure 1.15). The annual average surface temperature is getting warmer in recent years. The larger cladoceran, *D. mendotae*, had abundances that increased with the average surface temperature (r^2=0.45, p=0.0003). Three of the 8

species have abundances that decreased with the average surface temperature (*B. tubicen* r^2=0.68 with p<0.0001, *D. birgei* r^2=0.75 with p<0.0001 and *L. minutus* r^2=0.16 with p=0.0455). The remaining species had abundance that did not have any particular trend with the average surface temperature (*L. sicilis, D. thomasi* and *T.extensus*). *L. minutus* was the only copepod that had abundance that changed with the average surface temperature. Seven of the 8 species had abundances that could be significantly explained by using only the average surface temperature in regression models (Figure 1.16a,b). Only 3 species had polynomial fitted models (*B. tubicen*, *D. thomasi* and *T. extensus*). Average abundance of the majority of the species was best explained by a linear relationship with average surface water heating.

Ice-free season length for the sample dates that generally influenced average zooplankton abundance, even though it varied by only 35 days among all years (with averaged annual values ranging from 84 to 119 days) (Figure 1.17). Four of the 8 species had an abundance peak between 90 and 95 days (or 3 months) after the ice break-up (*D. mendotae, H. glacialis, L. sicilis,* and *L. minutus*). These species have abundances that increased after 3 months of ice-free waters and declined after this point. Of the remaining species, 3 of the 4 species have abundances that increased after 95 days after the first ice-break and had a larger range of days where their abundance was high (*B. tubicen, D. birgei* and *T. extensus*). In other words, the abundance of these species increases when the water has had a chance to warm up for over 3 months (or 95 days+ since ice-break) on average. *D. thomasi* abundance could not be explained by days since ice off. *T. extensus* was the only species with abundances that increased with more days

since ice-free (r^2=0.42, p=0.0004) (Figure 1.18b). All species abundance had a linear relationship with days since ice-free (Figure 1.18ab).

Each selected zooplankton species had abundance patterns that could be explained by some combination of *Bythotrephes* P/A, days since ice-break up and/or the average surface temperature (Table 1.3, Figure 1.19ab). *D. thomasi* was the only species that required a polynomial fit with the average surface temperature (Figure 1.19b). Five of the 8 species had abundance that was significantly explained by *Bythotrephes* P/A either alone or with another annual predictor (e.g., average surface temperature). *D. mendotae*, *H. glacialis* and *L. sicilis* had abundances that could be explained by *Bythotrephes* alone in a linear model (Figure 1.19ab). *L. minutus* and *D. thomasi* had abundance that was significantly explained by the average surface temperature (r^2=0.2138, p=0.0199; r^2=0.4781, p=0.0030, respectively) (Figure 1.19b). These species were less abundant in years with cooler epilimnia. *T. extensus* was the only species that had abundance that was explained by days since ice-break up in a linear regression model (r^2=0.3400, p=0.0024) (Figure 1.19b).

Objective 3: Does residual abundance correlate with the wind field over Harp Lake between 1980-2004?

With one exception, the residual abundance of the above regression models for the selected species was not correlated with wind speed or direction from 1980-2004 (Table 1.4, Figure 1.20). The exception was *D. mendotae*. For *D. mendotae*, there was a significant association between the residual abundance and the wind direction (r^2=0.2330, p=0.005) (Figure 1.21, refer to Appendix B1 for a further explanation of this

relationship between residual abundance and wind direction). When the residual abundances were lower for this species, the wind generally originated in a different range of directions than when positive residuals were observed. All correlations between the residual abundance and wind speed and direction can be found in Appendix C.

Discussion

All species had abundance that could be explained by *Bythotrephes* P/A, by annual averaged average surface temperature and/or by the dates of ice breakup each year. Those species whose long-term average abundance patterns were best explained by *Bythotrephes* alone (*D. mendotae, H. glacialis* and *L. sicilis*) were probably responding to the invasion by *Bythotrephes*. In 1993, *Bythotrephes* appeared in Harp Lake and affected the abundance of large and small cladocerans (Yan and Pawson 1997). Therefore, species that were affected by the invasion demonstrated a change (increase or decrease) in abundance between pre- and post-1993.

A polynomial fit for the annual regression models was appropriate for *D. thomasi*, perhaps likely because of the sensitivity of its phenology to summer heating. The average surface temperature was particularly important in this polynomial model. First, abundance could be anticipated based on the warming conditions. Second, the relationship between warming conditions and the abundance of this species was non-linear. An increase in temperature can lead to extra generations in a year by stimulating the early hatching of resting eggs (Chen and Folt 1996).

Despite the obvious effects of *Bythotrephes* P/A, the abundance of *L. minutus*, *D. thomasi* and *T. extensus* were only significantly correlated with average surface

temperature or days since ice-free. This suggests that these species were not influenced by *Bythotrephes* invasion in Harp Lake, as has also been observed in spatial surveys (Boudreau and Yan 2003). The long-term warming of Harp Lake is the predictor that best correlates with the abundance of these species. This may be because all these species are below the mixing layer. An increase in warmer waters would affect the long-term changes in lake physics denoted by earlier ice break-up, warmer epilimnia and life history stages.

Based on annual averages, predictions of zooplankton abundance were not improved significantly by considering the wind field in this lake. This result did not support with my predictions that some species would be significantly correlated with the wind field depending on their physical and behavioural characteristics (e.g., body size, strata location, and swim speed). According to Waife and Frid (1996), zooplankton are best viewed as 'passive drifters' that cannot swim against the wind-induced water current and are transported within the flow field. The animals can clearly swim, but not as fast or as strongly as the wind-induced current. Similarly, Sollberger and Paulson (1991) found that wind-induced currents could easily homogenize zooplankton distributions under turbulent mixing and aid in the transportation of zooplankton. However, it is possible that large, fast swimming animals such as *D. mendotae*, could out-swim the weaker currents when the wind speeds are slow and be concentrated downwind (Huber et al. 2011). With the exception of *D. mendotae*, all 7 species had residual abundance that could not be predicted by the wind field. *D. mendotae* is a large cladoceran that inhabits the hypolimnion during the daytime and returns to the surface during the night (Young

and Yan 2008). A possible reason why *D. mendotae* may have been the only species to show a significant association with wind direction may be due to thermocline tilting, which can cause animals in the hypolimnion to be distributed upward or concentrated downwind. However, this is unlikely since other species chosen in this study that inhabit the hypolimnion that are larger and faster than *D. mendotae* did not have a significant association with the wind direction (e.g., *L. sicilis*). This study has indicated that the wind field overpowers the swimming strength of the animals, even at low wind speeds (3-4 m/s, Zurek and Bucka 2004) but there may be chance occurrences where animals can actually withstand the hydrodynamics present in the lake.

The physical and behavioural characteristics of each species did not play a role in predicting abundance under the influence of the wind field. Surface water current speed is ~1.5 percent of the wind speed moving over the water (Haines and Bryson 1961). To hold a fixed position in the water against its movement, the animals would need to be able to swim at least 3.47 cm/s (corresponding with 2.32 m/s of wind speed), the slowest daily wind speeds observed over the study period. According to Zurek and Bucka (2004), weak winds are characterized as 3-4 m/s and the mobility of animals would depend on their swimming behaviour, physiology and anatomy. Almost 30% of the wind speeds on the sample date over Muskoka Airport were between 3-4 m/s during the study period. In fact, 77% of the wind speeds were <4 m/s, therefore the possibility that animals may be able to hold their position in the water is likely. However, based on the lack of pattern between the residual abundance and the wind field, the sustained swimming speed of the animals (average swim speed=0.199 cm/s) in this study must

have been lower than the current speed (even though the long-term wind speed was decreasing), and thus animals were downwelled if found in downwelling surface waters or upwelled to upper strata if found in the hypolimnion (Sollberger and Paulson 1991). It is also possible that the animals may become concentrated at the ends of the lake in the direction of the wind if the wind speed was very strong (Sollberger and Paulson 1991) but this does not seem to have influenced the data.

Wind speed was less important for predicting abundance compared to wind direction. The mean of all variance in residual abundance that could be explained by wind speed was 2.75%, less than the 5.25% that could be attributed to wind direction. The majority of 5.25% of the variance in residual abundance that could be attributed to wind direction was due to *D. mendotae*. The variance in residual *D. thomasi* abundance attributable to wind direction was 2.88%, much greater than that attributable to wind speed (0.88%). While not statistically significant, the relationship between the residual abundance and the wind direction suggests that zooplankton in Harp Lake may have changed their spatial distribution somewhat over time, at annual scales. They may have moved in a direction that better suits their preference for a particular depth (such as, resisting the water currents in the hypolimnion during the daytime to avoid predators, Herzig 1994).

In summary, two aspects of the annual overwater wind field (speed and direction) did not improve the prediction of long-term changes in zooplankton abundance at annual scales, when these data were generated fortnightly at a single, mid-lake station. Data from one station at the deepest portion of the lake was sufficient to indicate that the long-term

zooplankton abundance patterns vary annually, as previously shown (Yan et al. 2008). Yan et al. (2001) found that the zooplankton species in Harp Lake have indeed varied between 1978-1997, however, the present study documented long-term patterns beyond 1997 to 2004. Of the 8 species chosen in this study, only half had abundance that continued to follow the yearly trends observed from Yan et al. (2001). For instance, *D. mendotae* abundance continued to increase between 1997-2004, while *B. tubicen* and *D. birgei* abundance continued to decrease. However half of the species, *H. glacialis, L. sicilis* and *D. thomasi* abundance started decreasing. At the same time, *T. extensus* abundance began to increase. This is particularly surprising since *T. extensus* abundance declined in 1993 when *Bythotrephes* appeared (Yan and Pawson 1997). The reason for this could be that *T. extensus* populations have had the chance to replenish their numbers from the drastic decrease in 1993. *Bythotrephes* P/A did significantly correlate with the abundance of 5 of the 8 species chosen in the annual regression models (excluding *L. minutus*, *D. thomasi* and *T. extensus*). The presence of this invader in 1993 continued to affect the abundance of these 5 species beyond the time frame observed in Yan et al. (2001).

What has not been shown is that the species chosen in this study have abundances that can also be predicted based on the duration and heating of the ice-free season. The average surface temperature proved to be a significant predictor for 7 of the 8 species chosen (excluding *T. extensus*). This is not a surprise since many life stages are dependent on water temperature (Balcer et al. 1984). For example, *D. mendotae* abundance had a significant positive linear relationship with the average surface

temperature (r^2=0.50, p<0.0001), which indicates that this species is more abundant at warmer temperatures. However, *D. thomasi* abundance had a significant polynomial relationship with the average surface temperature (r^2=0.48, p=0.0030). In contrast to the average surface temperature, days since ice-free alone was not a significant predictor of abundance, with the exception of *T. extensus*. This lack of significance may arise because the overall range of days since ice-free (83.58-147) may not be large enough to notice a change in abundance. Therefore, using the average surface temperature alone as a measure to predict zooplankton abundance in Harp Lake may be useful for future analyses.

I chose to work on common species of zooplankton in Harp Lake that vary in size, swimming ability and depth preferences. My work suggests that these species can be used to quantify long-term changes in zooplankton at annual scales without consideration of the bias caused by changing wind fields. It is clear that the wind speed decreased over the study period and the wind direction shifted towards the north. Yet, zooplankton have not responded to these changes observed in the wind field at an annual average scale. Therefore, changing wind fields do not appear to have compromised our ability to detect the influence of other drivers such as *Bythotrephes* P/A (Yan et al. 2008) at annual scales. The greater interpretability of phytoplankton, fish, and benthos data requires an alternative explanation, at least at annually averaged scales (Arnott et al. 1998, Allen et al. 1999).

D. mendotae residual abundance was correlated with the wind direction using annual averages, but the other zooplankton species commonly found in the hypolimnion

during the day, *D. thomasi* and *L. siclis,* had no such association. In chapter 2, I examine whether a detailed inspection of seasonal changes in residual abundance patterns can clarify this result. Further insight may also be gathered by a more careful examination of the effect of the wind field on the thermocline, for animals that migrated between thermal layers. The wind effect within the thermocline is rather small and the turbulence level is diminished (Bengtsson 1973; Gorham and Boyce 1989; Elci 2008). The current speeds are thus low enough that directed animal movements might create patchiness within the metalimnion. Although wind effects on the long-term zooplankton data did not appear at annual scales, it remains to be seen if the same pattern is true at daily scales.

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Table 1.1: Physical and behavioural characteristics of the selected freshwater crustacean zooplankton from Harp Lake, Ontario. Blanks indicate unknown information.

Species	Mean body length (cm)	Swim speed (cm/s)	Vertical Migratory Behaviour (e.g., day/night, strata)	Food Size Range (μm)	Feeding method
Cladocerans					
Daphnia galeata mendotae	0.092	0.120[1]	Day (Hypolimnion)[3] Night (Epilimnion)[3]	1.1-20[2]	Filtration[2]
Holopedium glacialis	0.068	Very slow[4]	Day (Epilimnion/Metalimnion)[10] Night (Hypolimnion)[10]	4.0-25[2]	Filtration[2]
Bosmina tubicen	0.038	0.408[6]	Day (Epilimnion)[3] Night (Metalimnion)[3]		
Diaphanosoma birgei	0.059	0.150[13]	Day (Epilimnion/Metalimnion)[11] Night (Epilmnion/Metalimnion)[11]		Filtration[2]
Copepods, Calanoids					
Leptodiaptomus sicilis	0.132	0.168[1]	Day (Hypolimnion)[3] Night (All depths)[3]	5-50[2]	Stationary suspension[2]
Leptodiaptomus minutus	0.089	0.340[1]	Day (Epilimnion/Metalimnion)[9] Night (Epilmnion/Metalimnion)[9]		Stationary suspension[2]
Copepods, Cyclopoids					
Diacyclops bicuspidatus thomasi	0.087	0.170[1]	Day (Hypolimnion)[12] Night (Epilimnion/Metalimnion)[12]	15-100[2]	Omnivore carnivore[2]
Tropocyclops extensus	0.050	0.035[8]	Day (Hypolimnion)[12] Night (Epilimnion/Metalimnion)[12]	6.5-80[2]	Omnivore carnivore[2]

[1]Muirhead and Sprules 2003; [2]Barnett et al. 2007; [3]Young and Yan 2008; [4]Link 1996; [5]Young et al. 2009; [6]Lagergren et al. 1997; [7]Strecker and Arnott 2008; [8]Dieguez and Gilbert 2002; [9]Cooke et al. 2008; [10]Tessier 1983 and Warvagen and Nilssen 2011;[11]Doulka and Kebayias 2008; [12]Barbiero et al. 2005; [13]Ramcharan and Sprules 198.

Table 1.2: Regression models using the average abundance of zooplankton species and *Bythotrephes* P/A (Bytho).

Species	**Model**	**r^2**	**p-value**
D. mendotae	LogAbundance = 2.315 + 0.5708*Bytho	0.62	<0.0001
H. glacialis	LogAbundance = 2.121 + 0.4199*Bytho	0.27	0.0076
B. tubicen	LogAbundance = 2.527 - 1.276*Bytho	0.55	<0.0001
D. birgei	LogAbundance = 2.781 - 1.801*Bytho	0.64	<0.0001
L. sicilis	LogAbundance = 1.314 + 0.7874*Bytho	0.54	<0.0001
L. minutus	A significant model could not be generated using *Bythotrephes* P/A	---	---
D. thomasi	A significant model could not be generated using *Bythotrephes* P/A	---	---
T. extensus	LogAbundance = 2.65 - 0.2821*Bytho	0.16	0.0457

Table 1.3: Models using the average abundance of zooplankton species using stepwise multiple regressions with an annual predictor: *Bythotrephes* P/A (Bytho), days since ice-free (Free), and average surface temperature (AST).

Species	**Model**	**r^2**	**p-value**
D. mendotae	LogAbundance = 2.315 + 0.5708*Bytho	0.62	<0.0001
H. glacialis	LogAbundance = 2.121 + 0.4199*Bytho	0.27	0.0076
B. tubicen	LogAbundance = 4.561 - 0.8354*Bytho - 0.1578*AST	0.65	<0.0001
D. birgei	LogAbundance = 6.82 - 0.937*Bytho - 0.3133*AST	0.90	<0.0001
L. sicilis	LogAbundance = 1.314 + 0.7874*Bytho	0.54	<0.0001
L. minutus	LogAbundance = 3.479 - 0.0487*AST	0.21	0.0199
D. thomasi	LogAbundance = -46.82 + 10.46*AST - 0.7323*AST^2 + 0.01684*AST^3	0.48	0.0030
T. extensus	LogAbundance = 0.8918 + 0.01555* Free	0.34	0.0024

Table 1.4: Squared part/parital correlation coefficients between the residual abundance of zooplankton from the models in Table 1.3 and the wind field. Significance denoted by a p-value<0.05 and an asterisk. The top number is the part correlation and the bottom number is the partial correlation coefficients.

Zooplankton Species	Wind Speed[a] (m/s)		Wind Direction[b] (degrees)	
	Squared Coefficient of Determination (r^2)	**p-value**	**Squared Coefficient of Determination (r^2)**	**p-value**
D. mendotae	0.0441 0.0733	0.3137 0.2006	0.2330	0.005*
H. glacialis	0.0064 0.0061	0.7039 0.7161	0.0010	0.977
B. tubicen	0.0345 0.0207	0.4080 0.5449	0.0188	0.700
D. birgei	0.0265 0.0787	0.4807 0.2446	0.0041	0.928
L. sicilis	0.0223 0.0127	0.4859 0.6176	0.0213	0.640
L. minutus	0.0002 0.0003	0.9510 0.9413	0.0055	0.885
D. thomasi	0.0056 0.0088	0.7219 0.6781	0.1005	0.108
T. extensus	0.0162 0.0169	0.5445 0.5451	0.0357	0.457

[a]Part/partial Pearson correlation coefficients (presented as the coefficient of determination, squared correlation coefficient) using Analyse-it add on for Excel
[b]Bivariate linear-circular association coefficients squared using Oriana 3.0

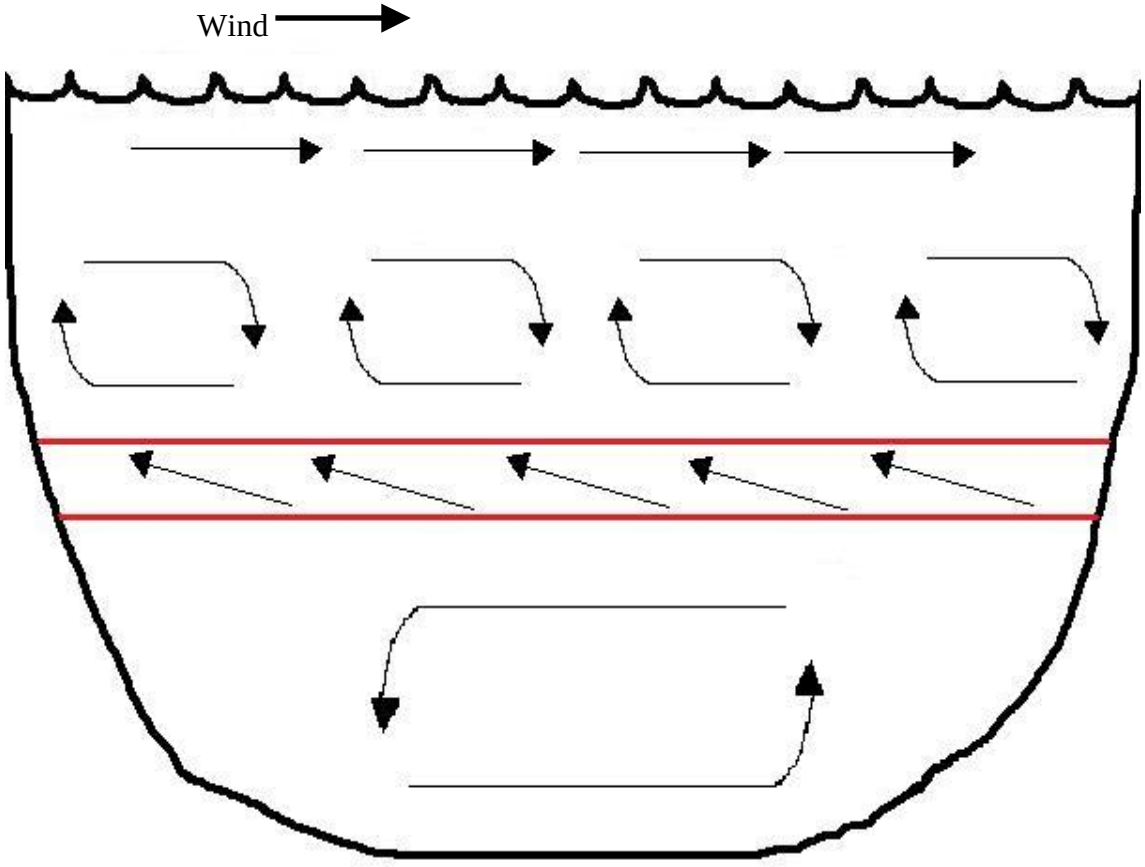


Figure 1.1: A simplified schematic representation of the water movement in a stratified lake. There are 3 distinct strata indicated: above the upper gray line, the epilimnion; within the gray lines, the metalimnion/thermocline; and below the lower gray line, the hypolimnion.

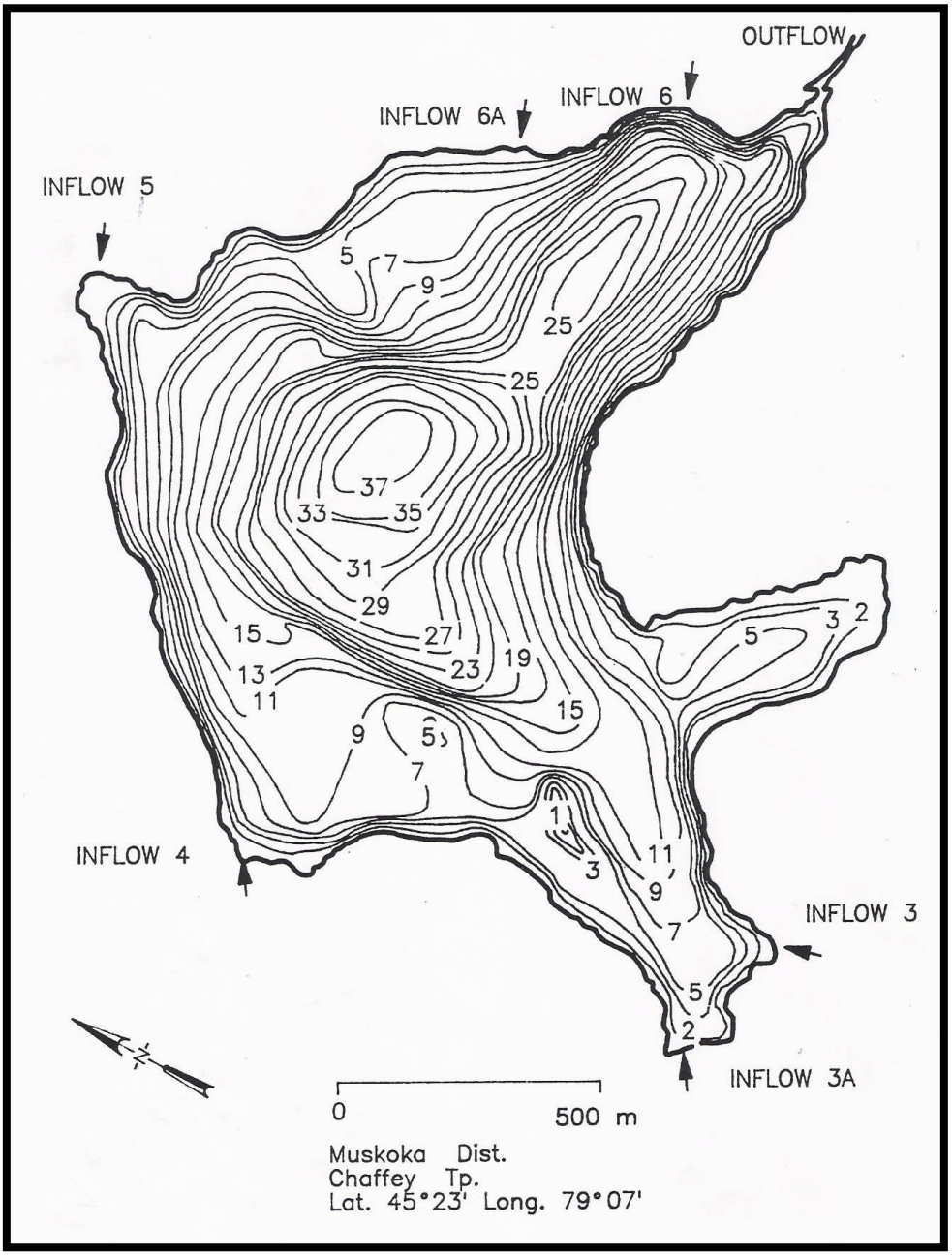


Figure 1.2: Bathymetric map of Harp Lake, Ontario. Contours are shown in meters.

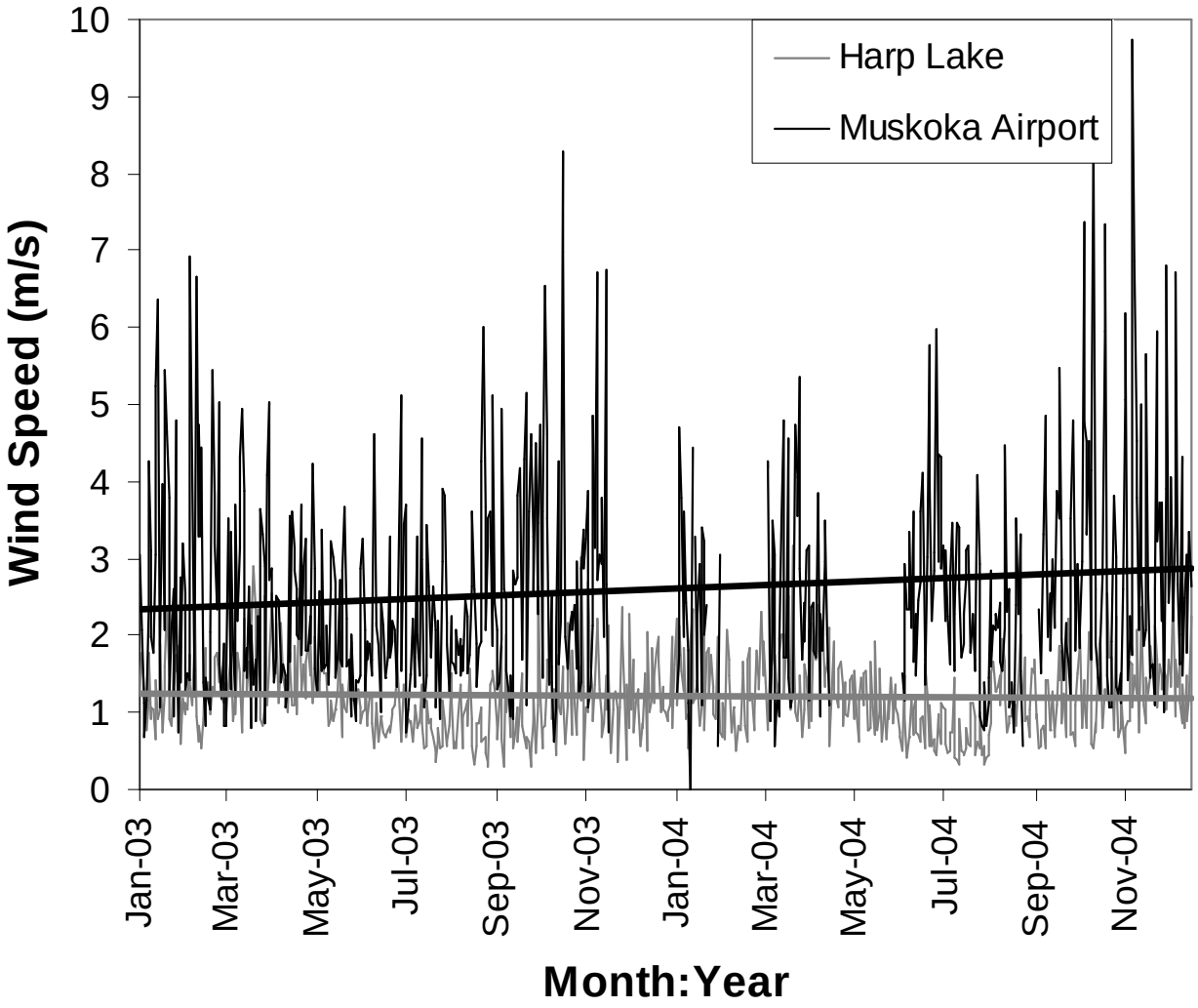


Figure 1.3: The daily wind speeds from Harp Lake and Muskoka Airport between 2003-2004. The thick gray line indicates the regression line for Muskoka Airport (r^2=0.0139). The black thick line indicates the regression line for Harp Lake (r^2=0.0020).

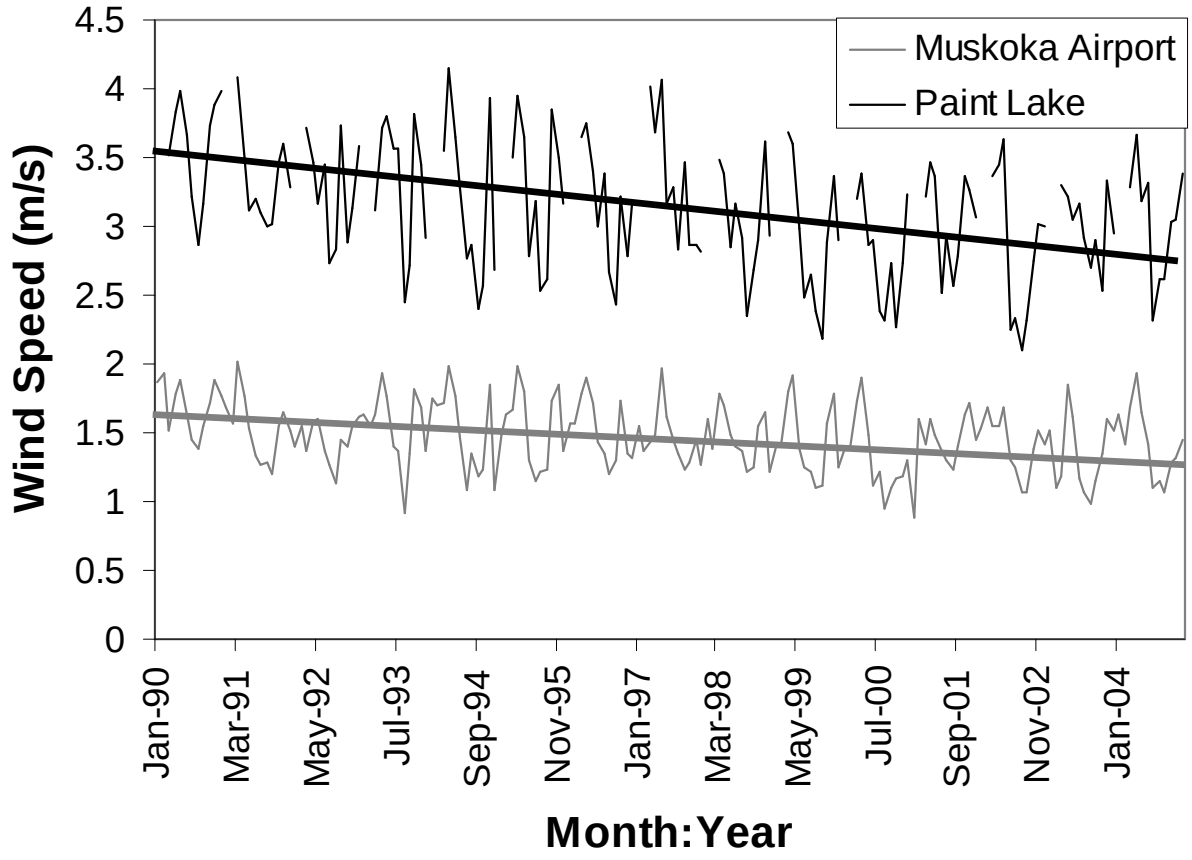


Figure 1.4: The monthly wind speeds from Paint Lake and Muskoka Airport between 1990-2004. The thick gray line indicates the regression line for Muskoka Airport (r^2=0.0861). The black thick line indicates the regression line for Paint Lake (r^2=0.1447).

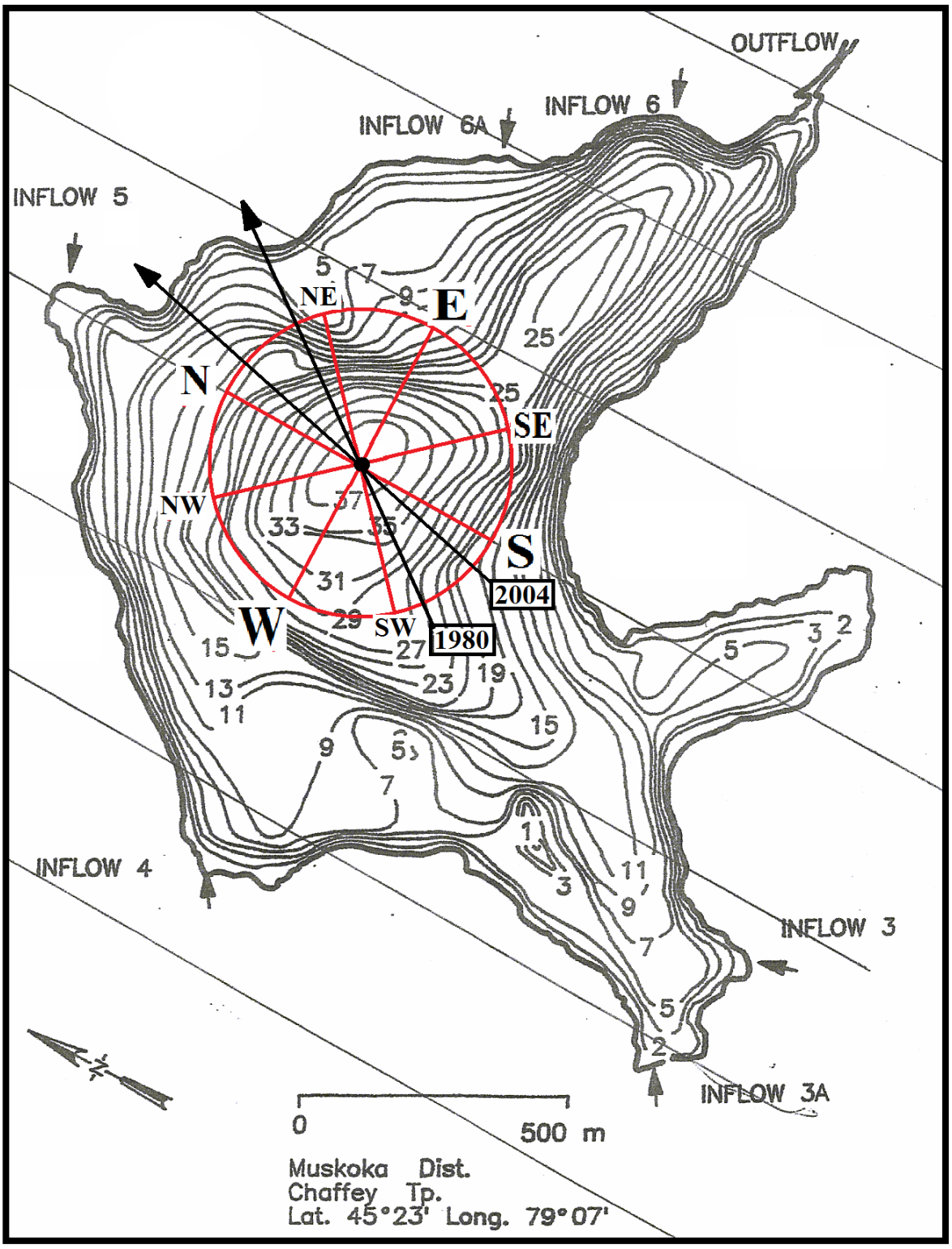


Figure 1.5: Bathymetric map of Harp Lake, Ontario with an overlay of a standard compass rose diagram in the direction of true North. The sampling station is indicated by a black circle at the deepest portion of the lake. The wind directions are shown separately for 1980 and 2004.

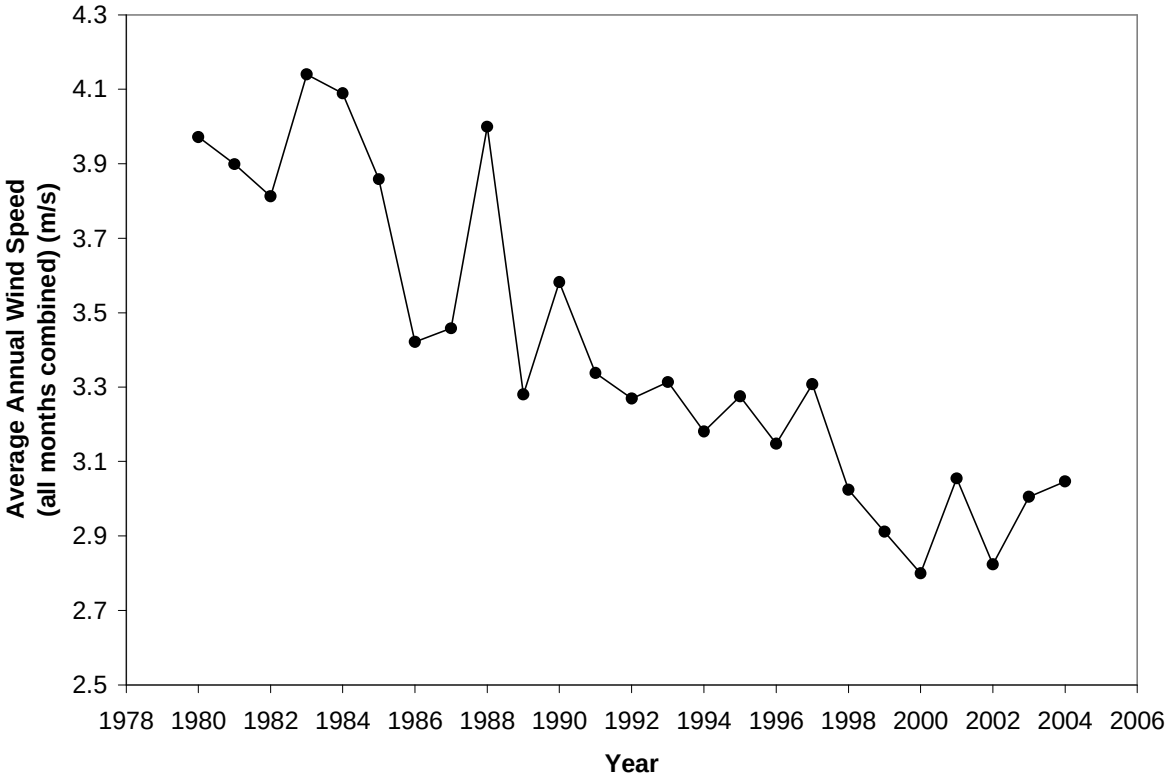
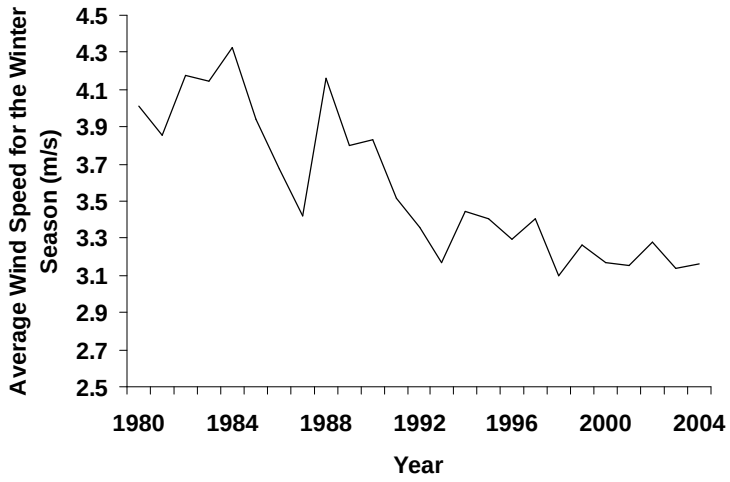


Figure 1.6: Long-term trends in average annual wind speed for all months combined from 1980-2004 at the Muskoka Airport, Ontario, Canada.

A)



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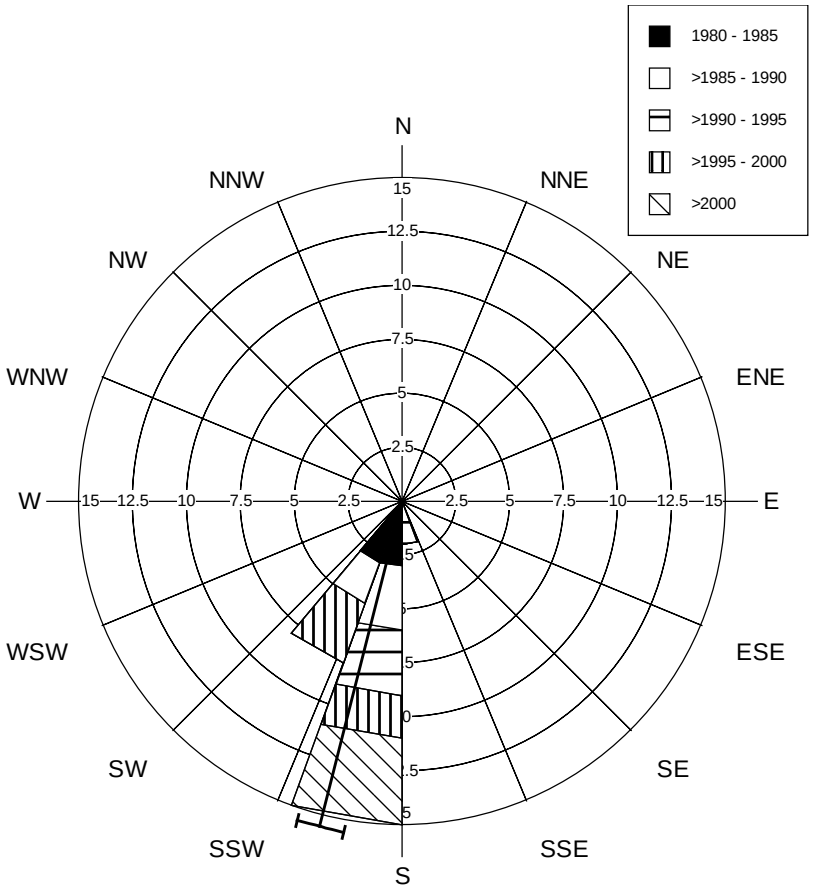
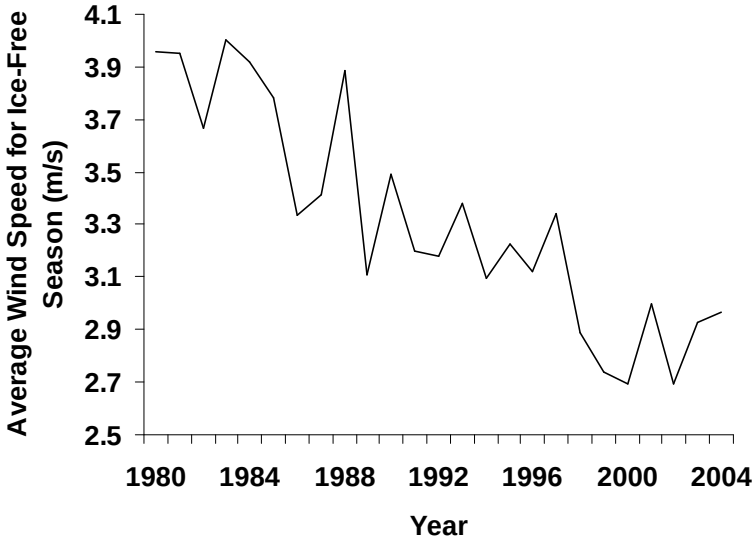


Figure 1.7: Summary of winter wind fields (November to March) from 1980-2004 over Muskoka Airport. A) Linear plot depicting the average yearly wind speed for the winter season. B) Two-variable rose histogram depicting the average yearly wind direction (compass direction) for the winter season where the single vertical arrow is the mean wind direction (generated using Oriana 3.0).

A)



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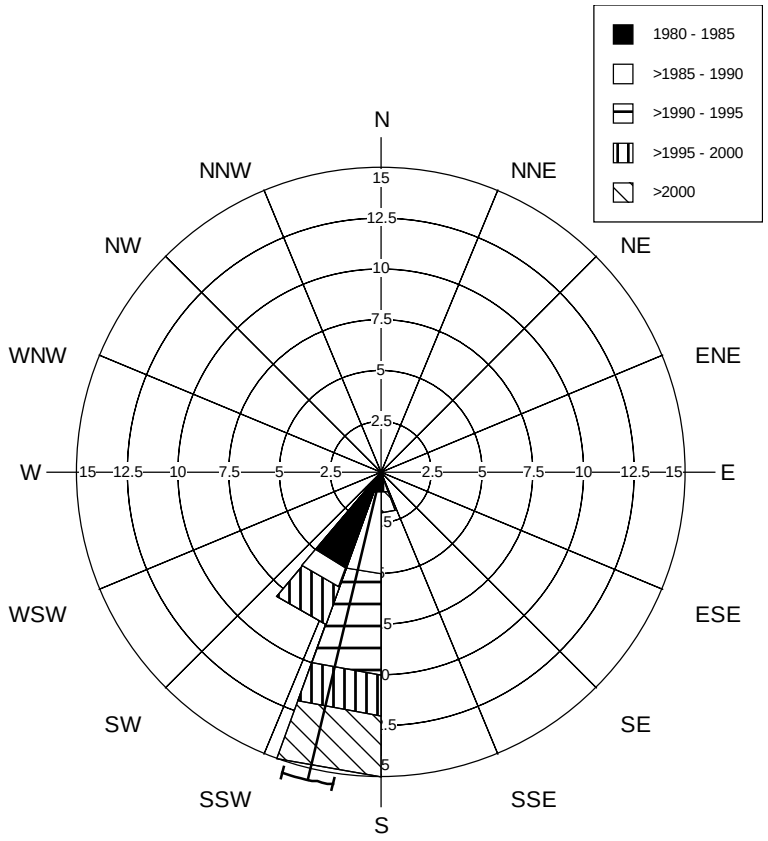


Figure 1.8: Summary of ice-free wind fields (April to October) from 1980-2004 over Muskoka Airport. A) Linear plot depicting the average yearly wind speed for the ice-free season. B) Two-variable rose histogram depicting the average yearly wind direction (compass direction) for the ice-free season where the single vertical arrow is the mean wind direction (generated using Oriana 3.0).

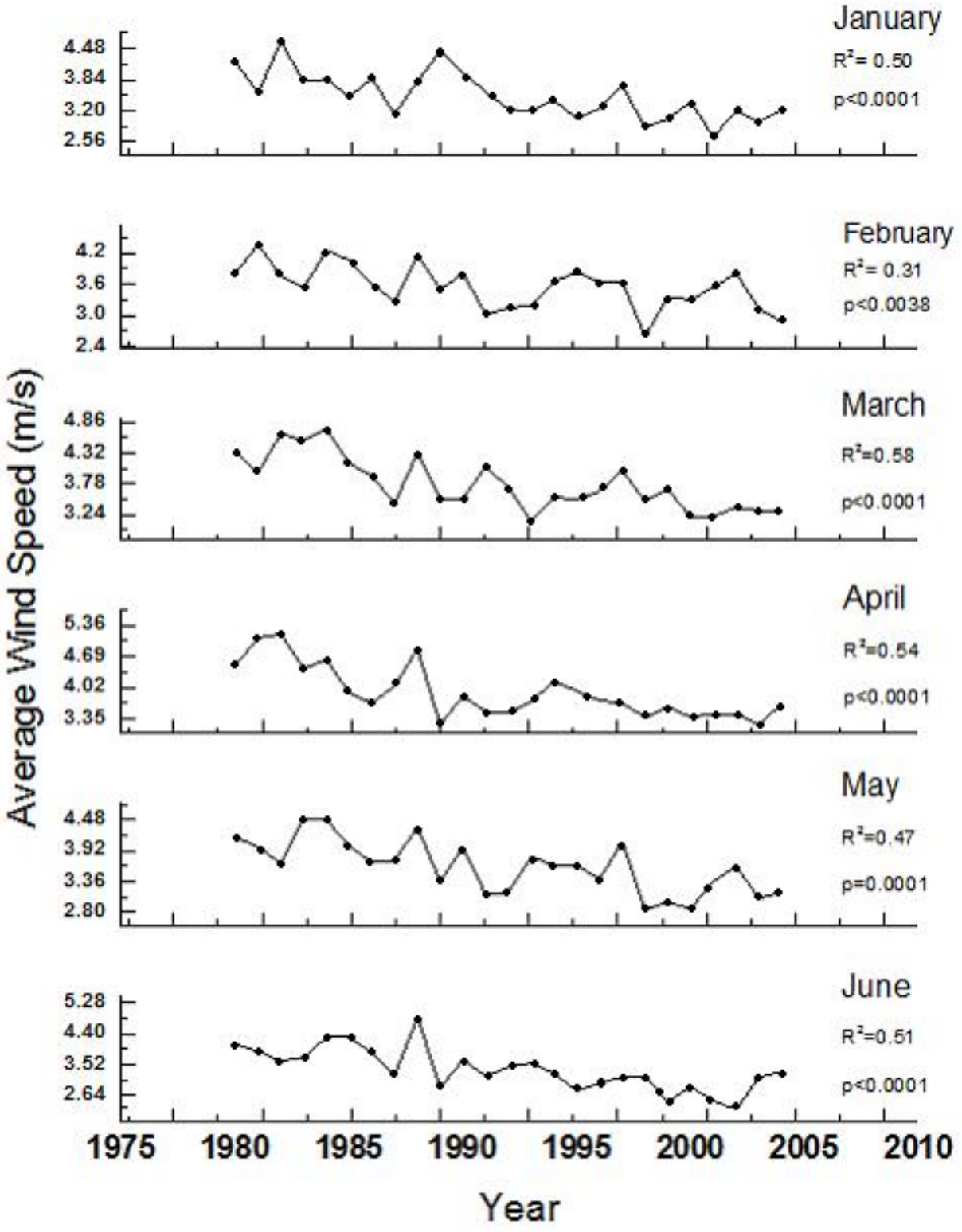


Figure 1.9a: Long-term trends in average monthly wind speed from 1980-2004 at the Muskoka Airport, Ontario, Canada.

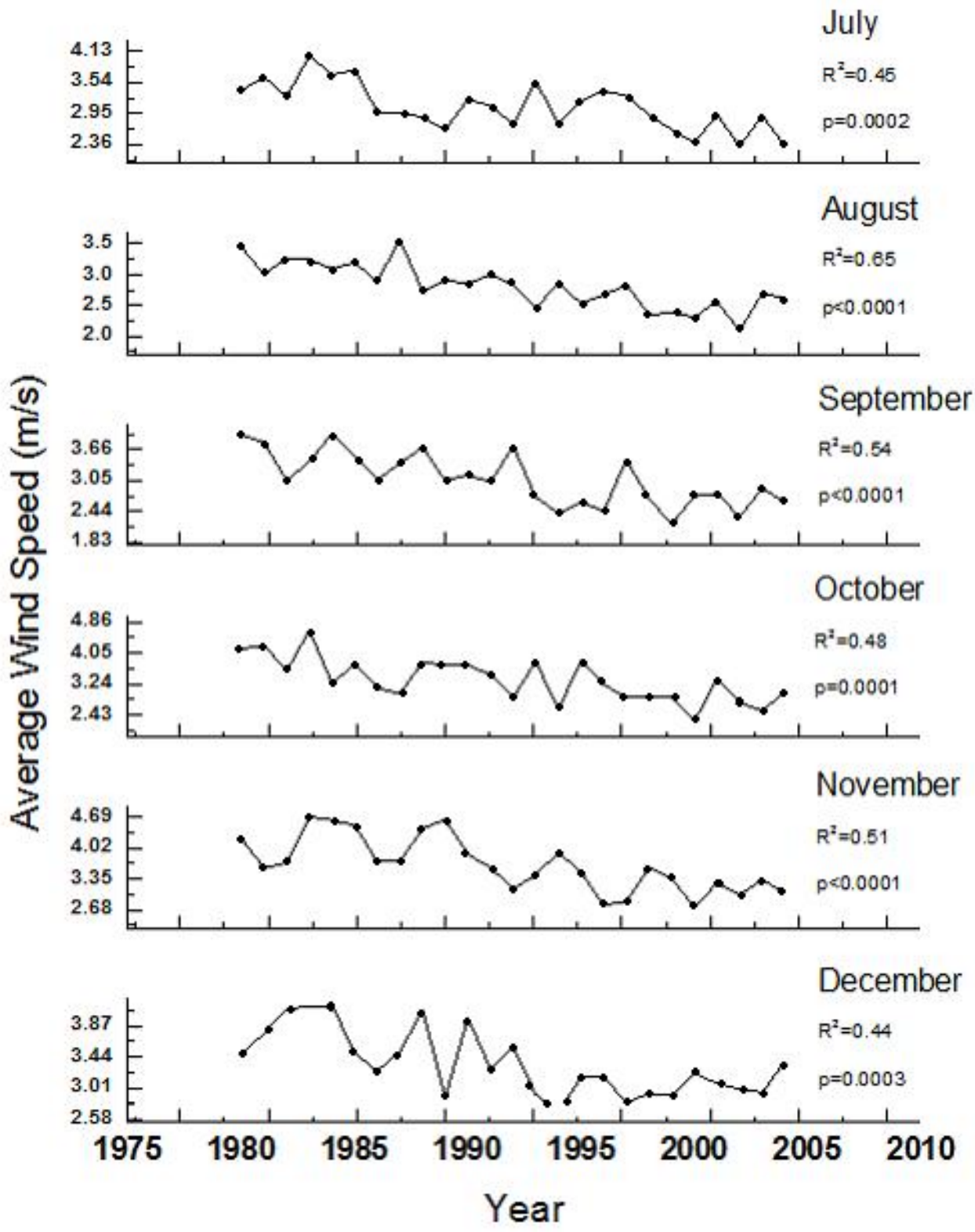


Figure 1.9b: Long-term trends in average monthly wind speed from 1980-2004 at the Muskoka Airport, Ontario, Canada.

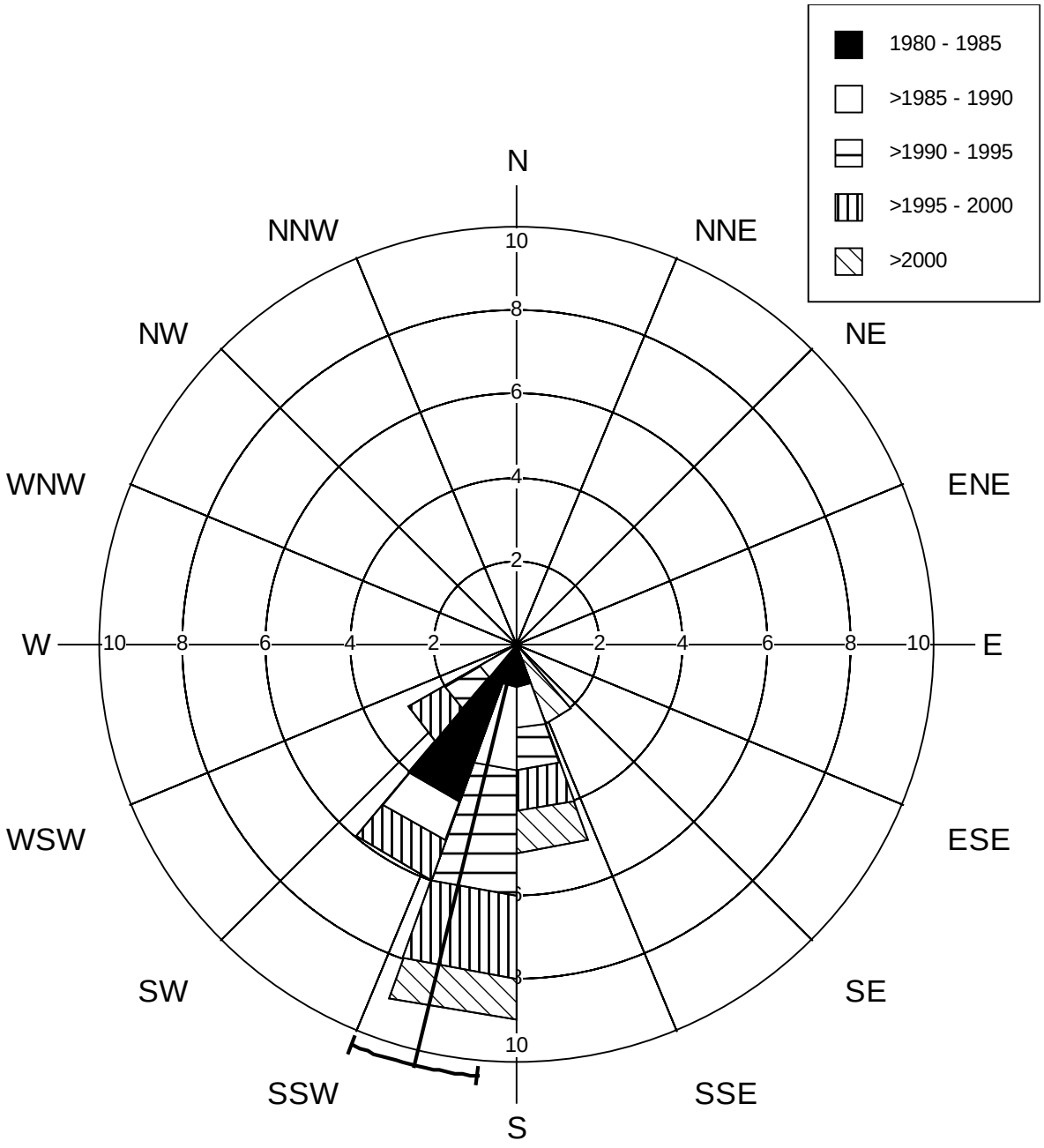


Figure 1.10: Two-variable rose histogram depicting the average yearly wind direction (compass directions) for all months combined from 1980-2004 at the Muskoka Airport, Ontario, Canada. The plots were generated using Oriana 3.0.

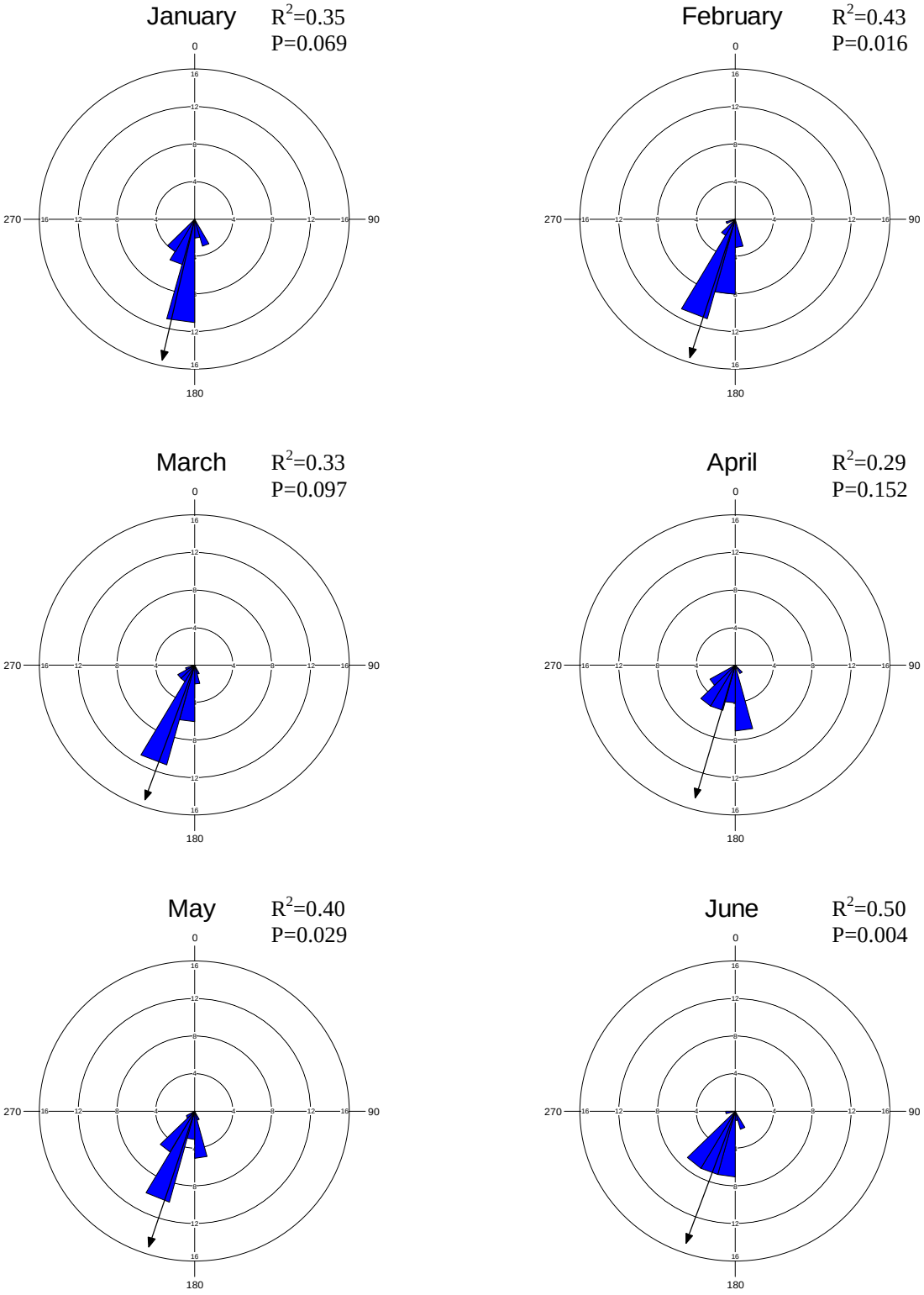


Figure 1.11a: Rose plots depicting the average yearly wind direction (degrees) for each month from 1980-2004 at the Muskoka Airport, Ontario, Canada. The single vertical arrow is the mean wind direction. The wedges depict the frequency of wind directions during the time span from that particular wind direction. The rose plots were generated using Oriana 3.0.

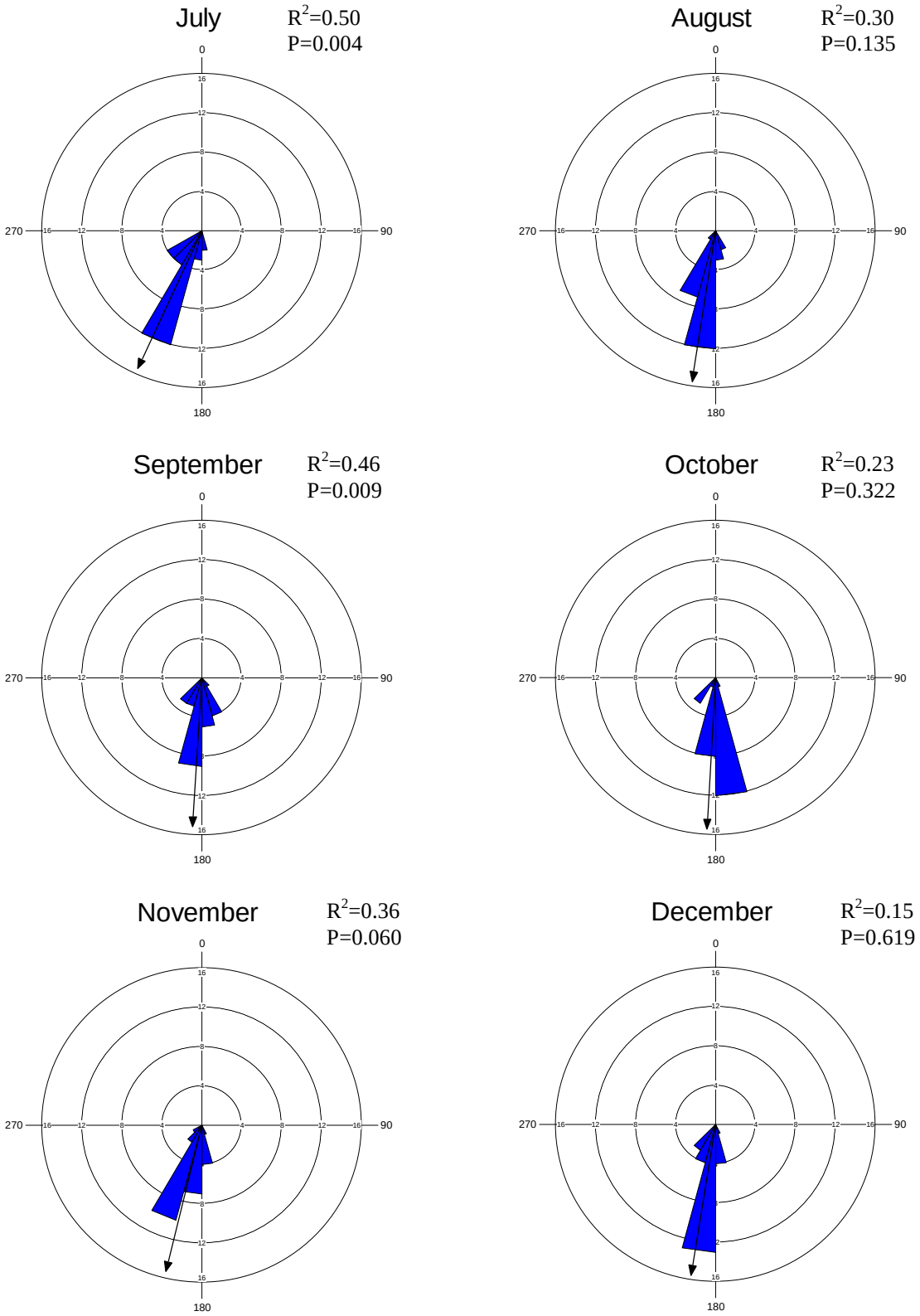


Figure 1.11b: Rose plots depicting the average yearly wind direction (degrees) for each month from 1980-2004 at the Muskoka Airport, Ontario, Canada. The single vertical arrow is the mean wind direction. The wedges depict the frequency of wind directions during the time span from that particular wind direction. The rose plots were generated using Oriana 3.0.

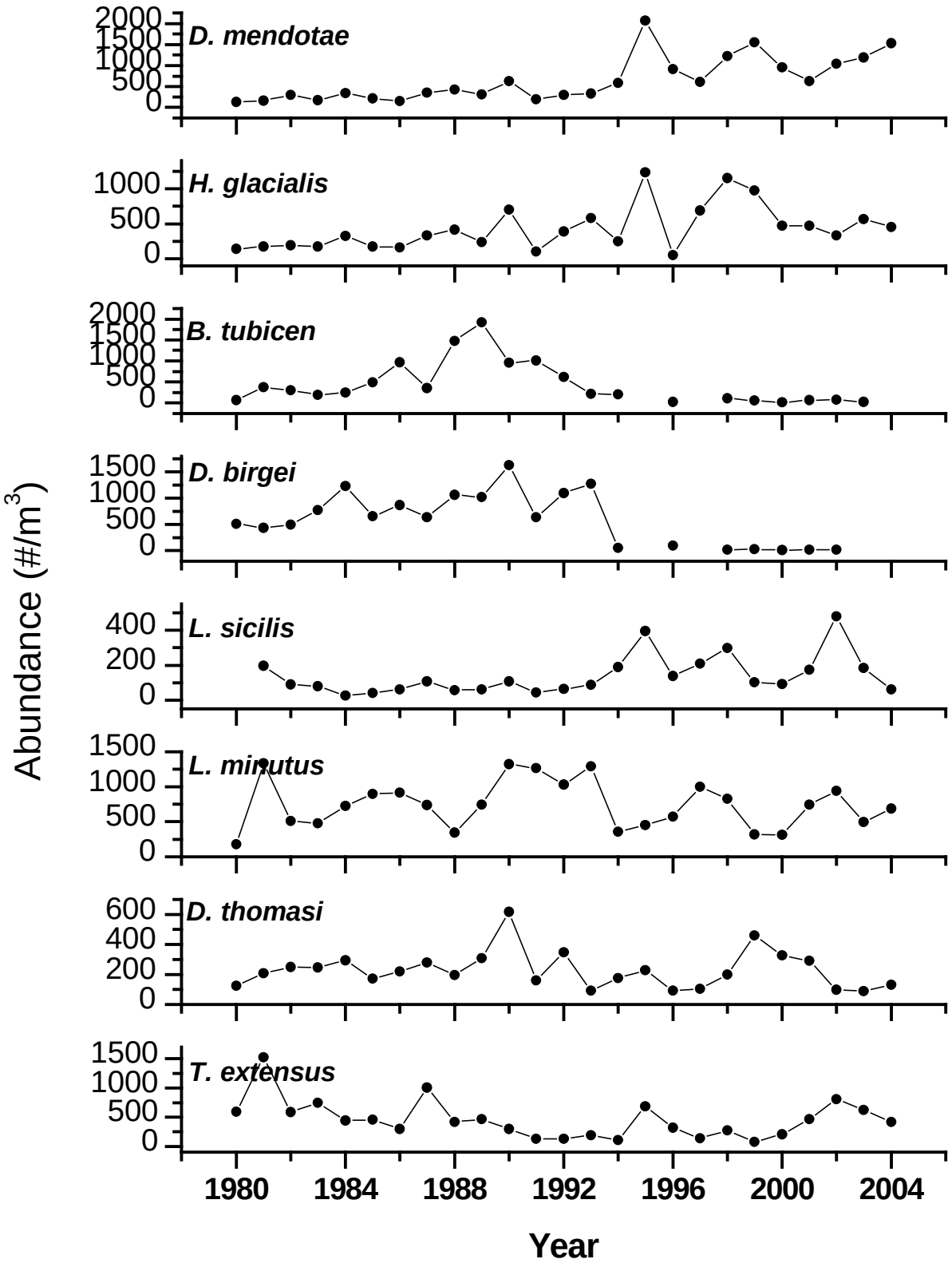


Figure 1.12: The long-term trends in average annual abundance of the selected zooplankton species in Harp Lake, Ontario.

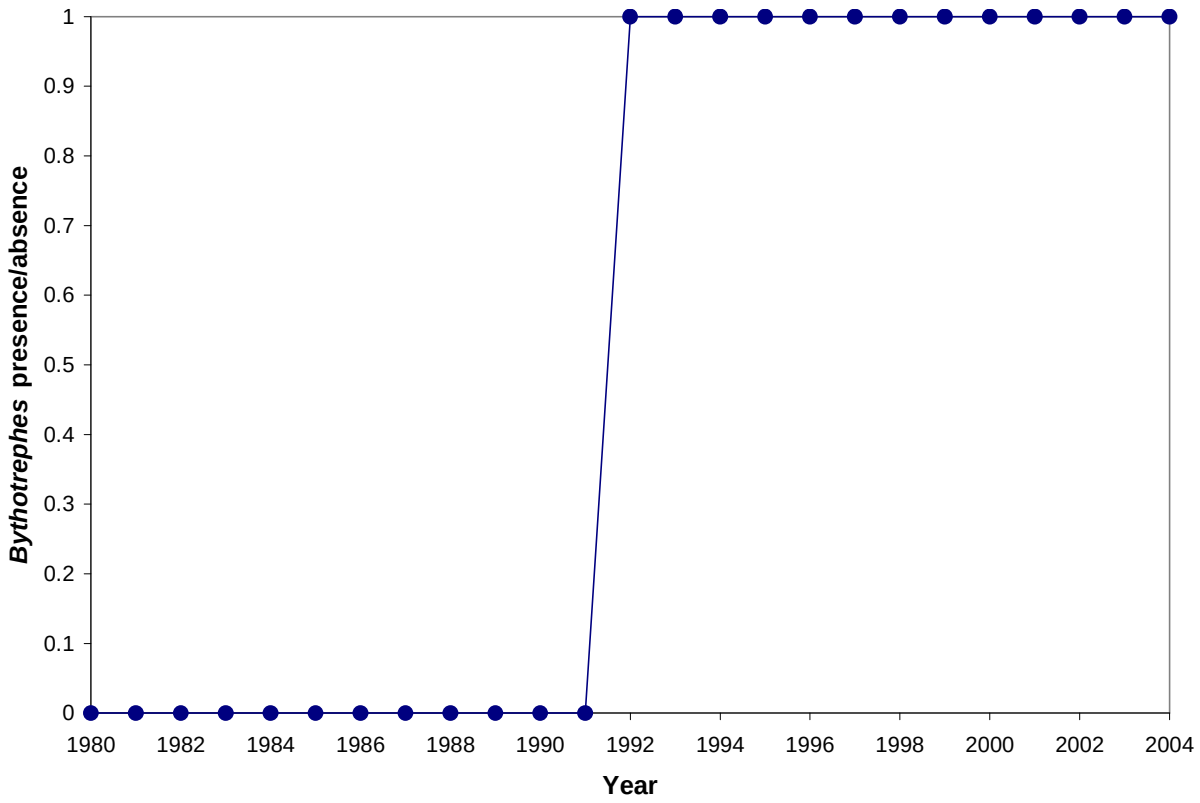


Figure 1.13: The presence/absence of *Bythotrephes* in Harp Lake, Ontario between 1980-2004.

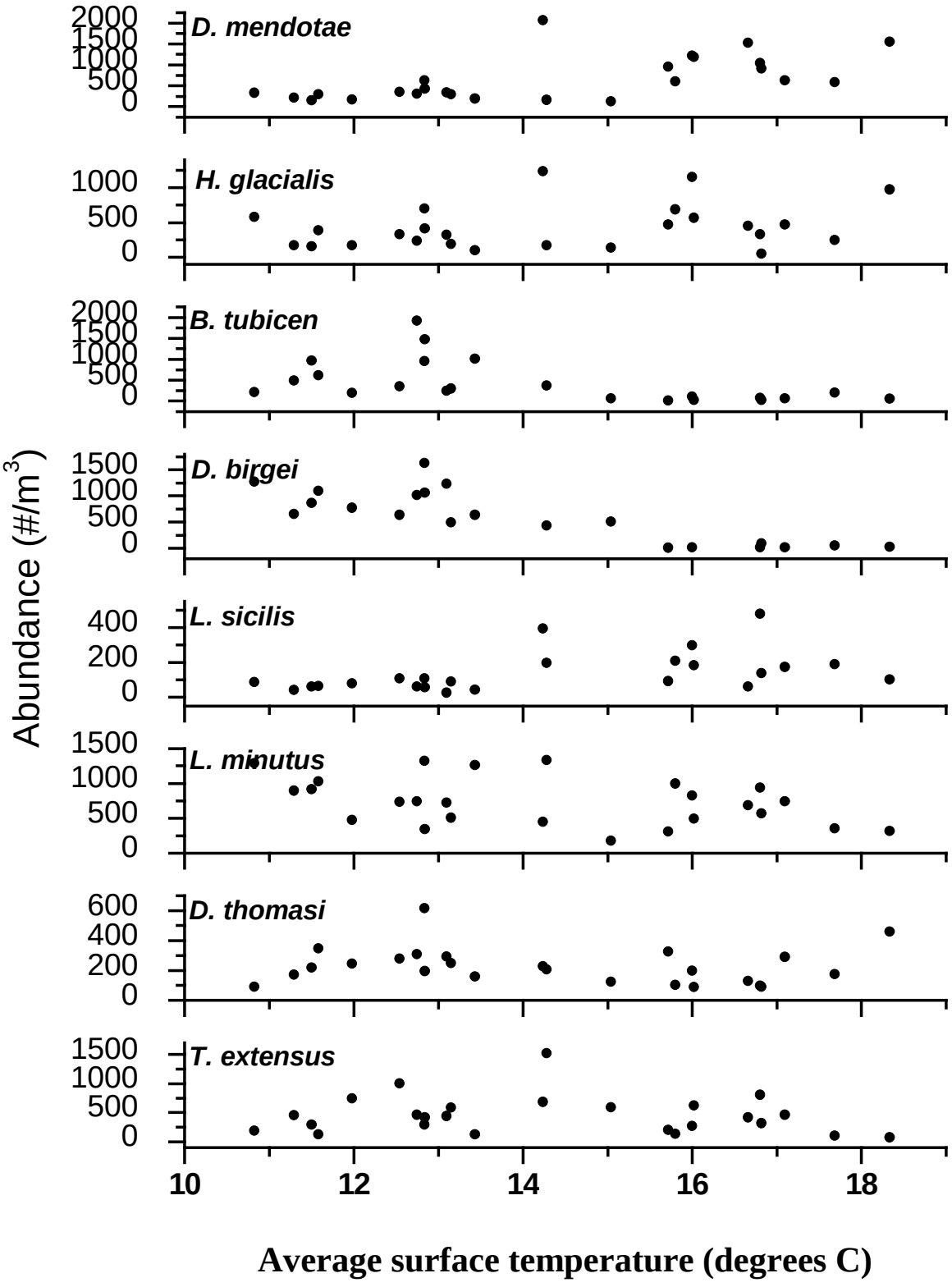


Figure 1.14: The long-term trends in average annual abundance versus average surface temperature of the selected zooplankton species in Harp Lake, Ontario.

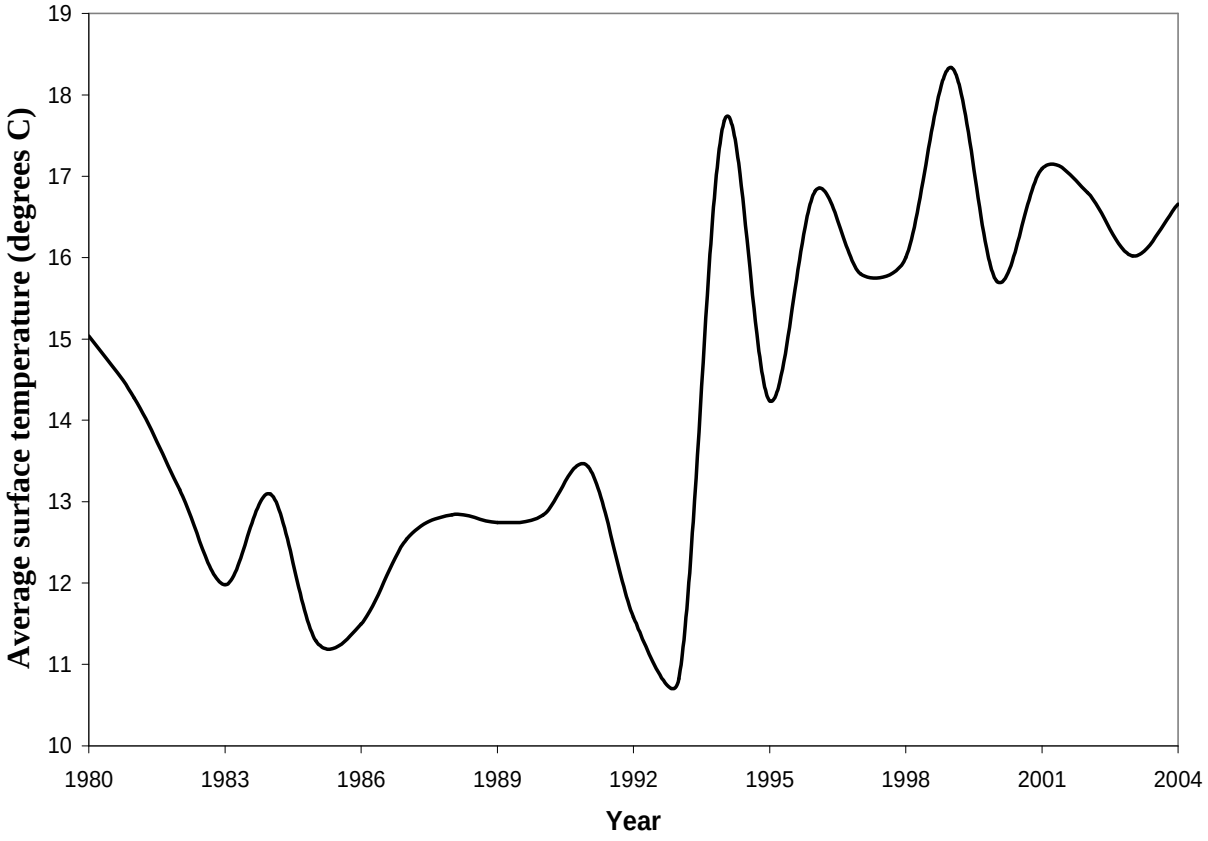


Figure 1.15: The average surface temperature in Harp Lake, Ontario from 1980-2004.

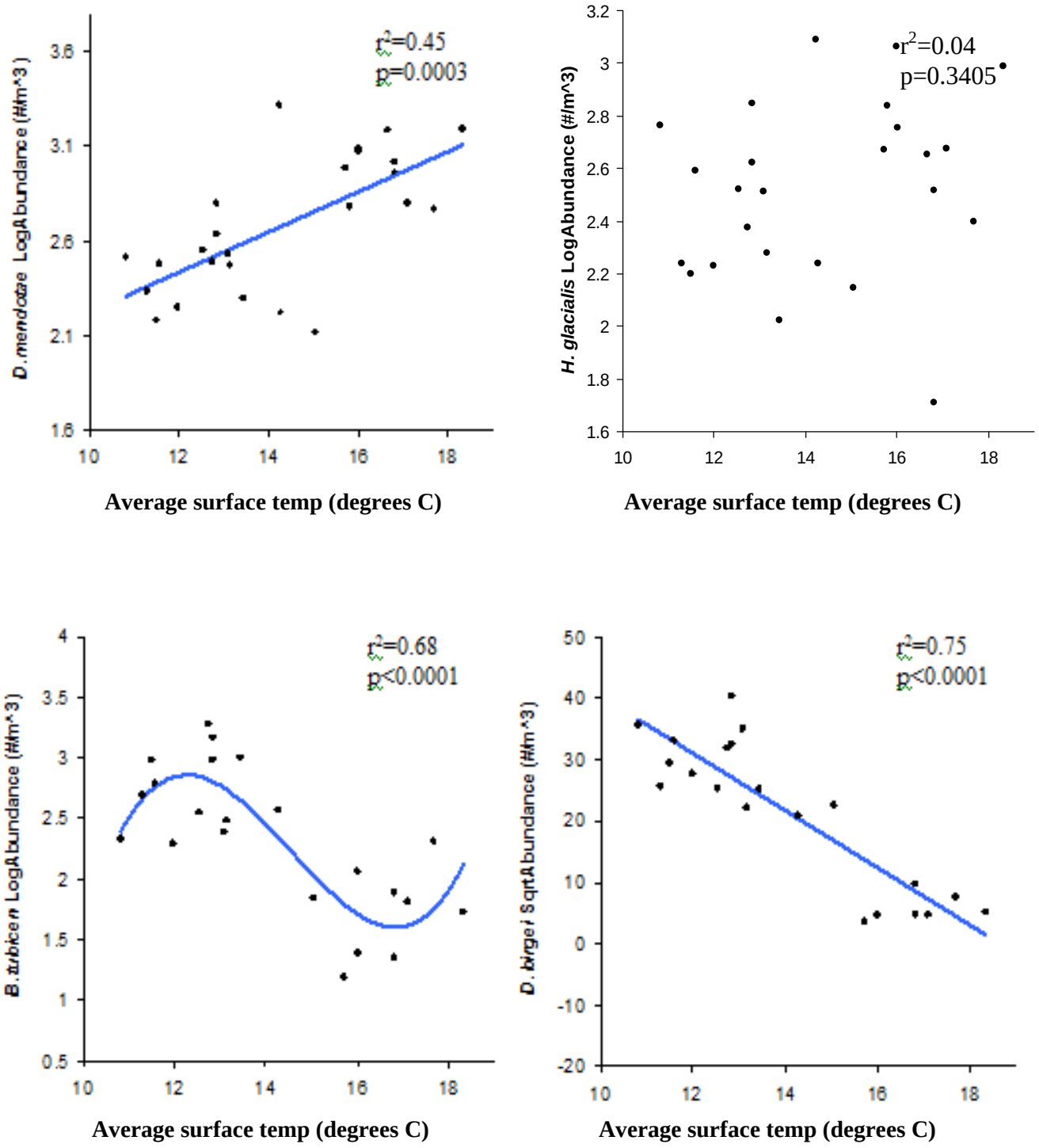


Figure 1.16a: Least squares regression models predicting the average annual abundance of the selected zooplankton species abundance with respect to the average surface temperature in Harp Lake, Ontario.

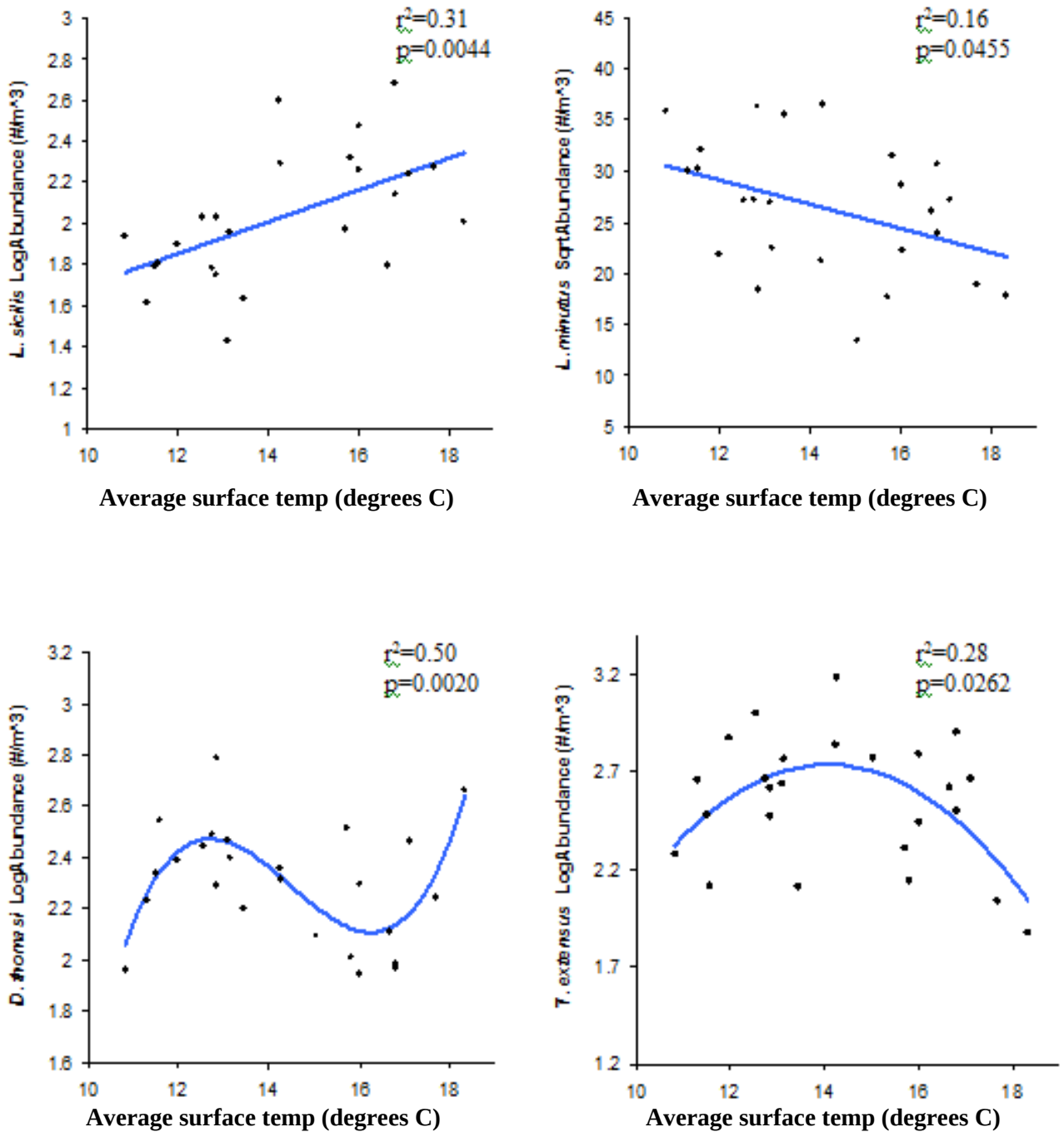


Figure 1.16b: Least squares regression models predicting the average annual abundance of the selected zooplankton species abundance with respect to the average surface temperature in Harp Lake, Ontario.

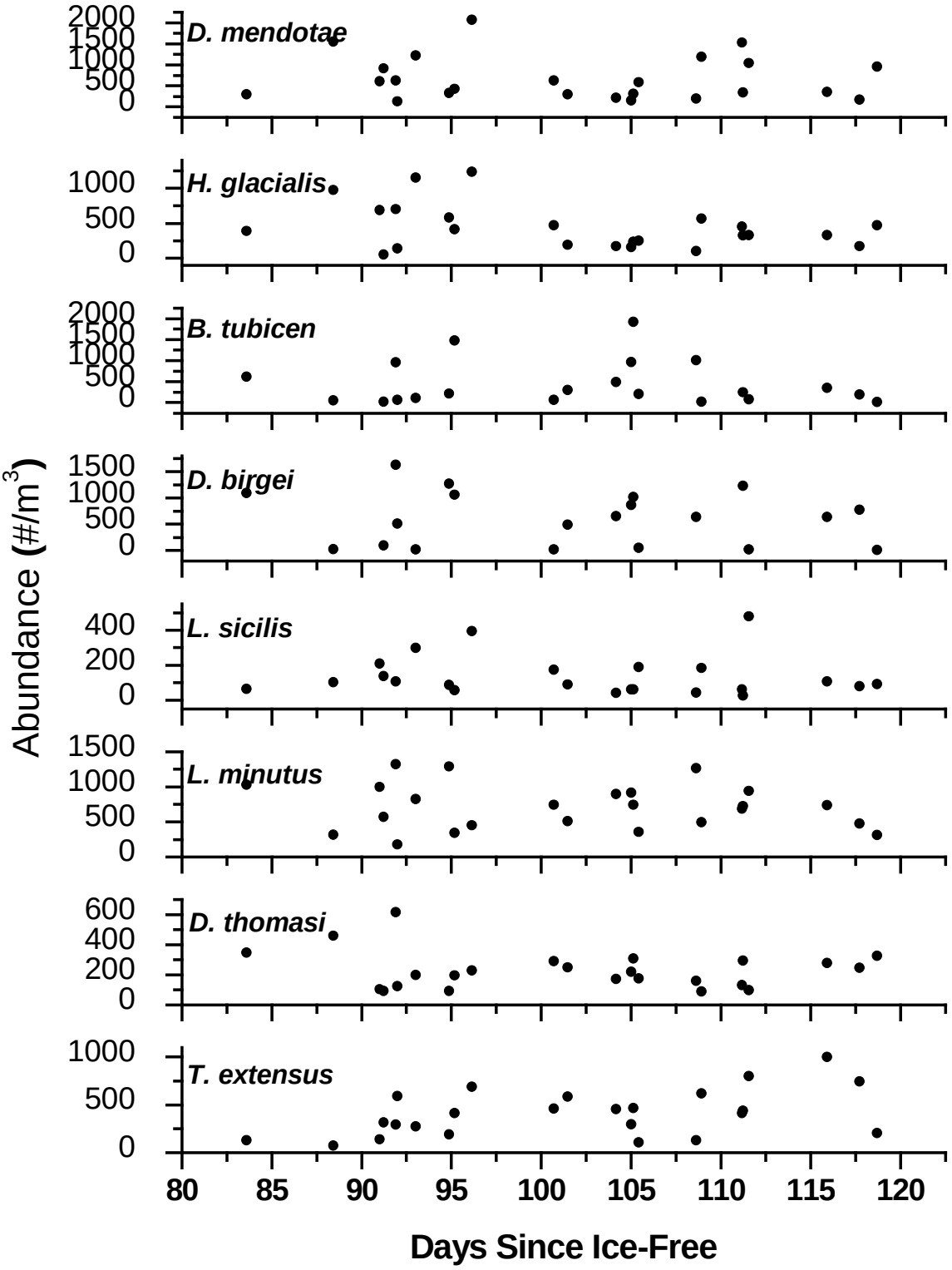
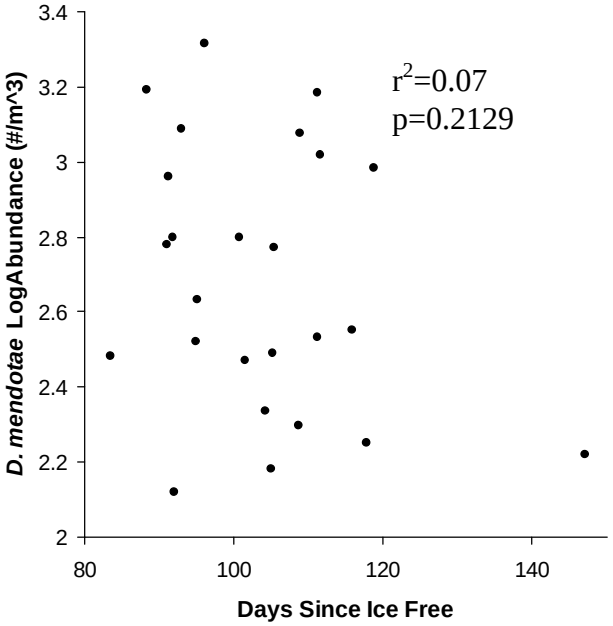
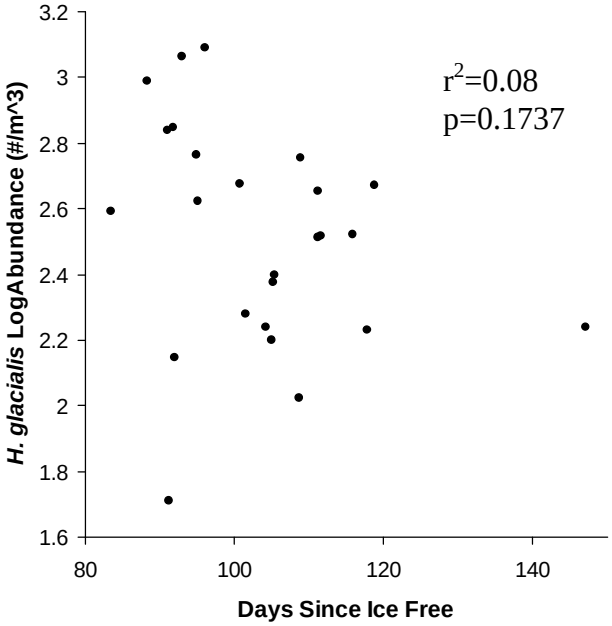
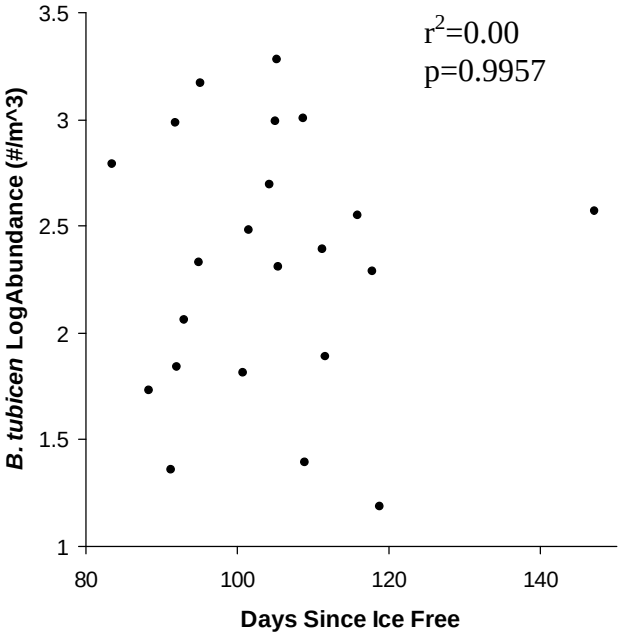


Figure 1.17: The long-term trends in abundance as a function of the annual average of days since ice free of the selected zooplankton species in Harp Lake, Ontario.







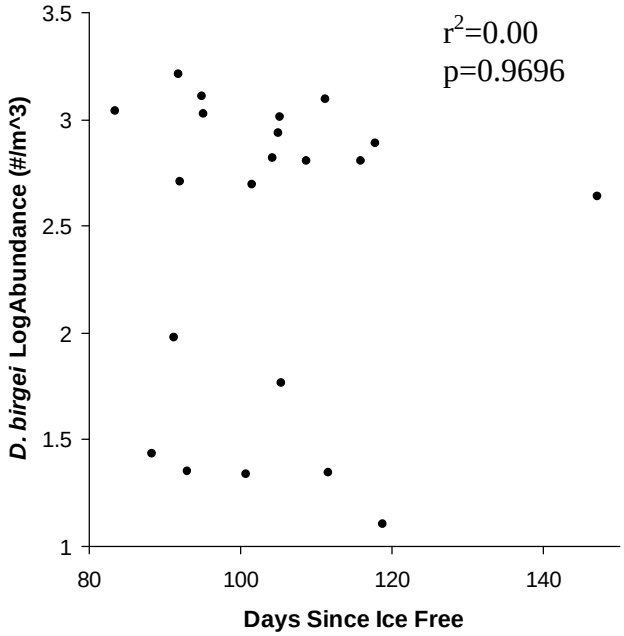


Figure 1.18a: Least squares regression models predicting the average annual abundance of the selected zooplankton species abundance with respect days since ice-free.

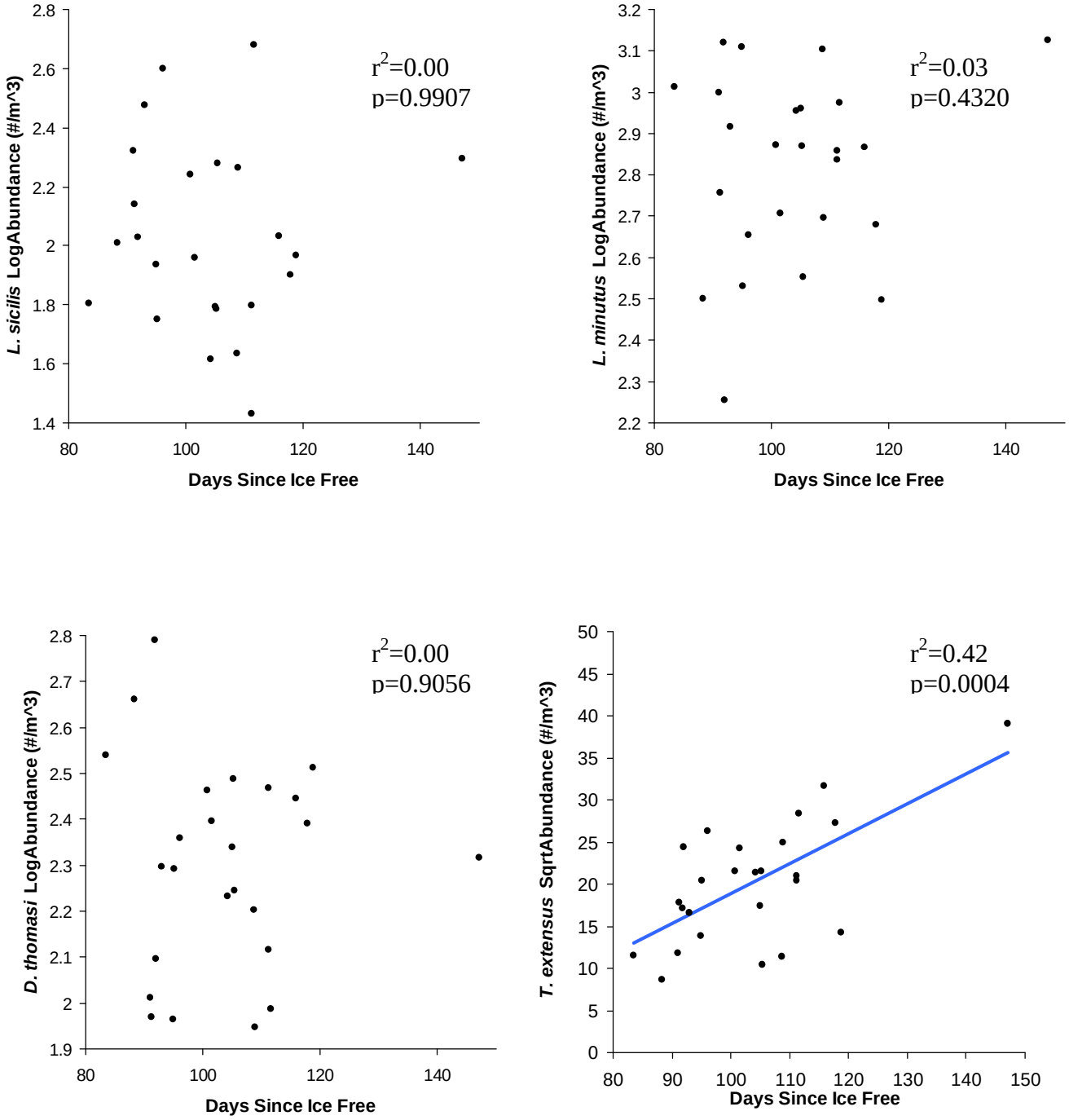


Figure 1.18b: Least squares regression models predicting the average annual abundance of the selected zooplankton species abundance with respect to days since ice-free.

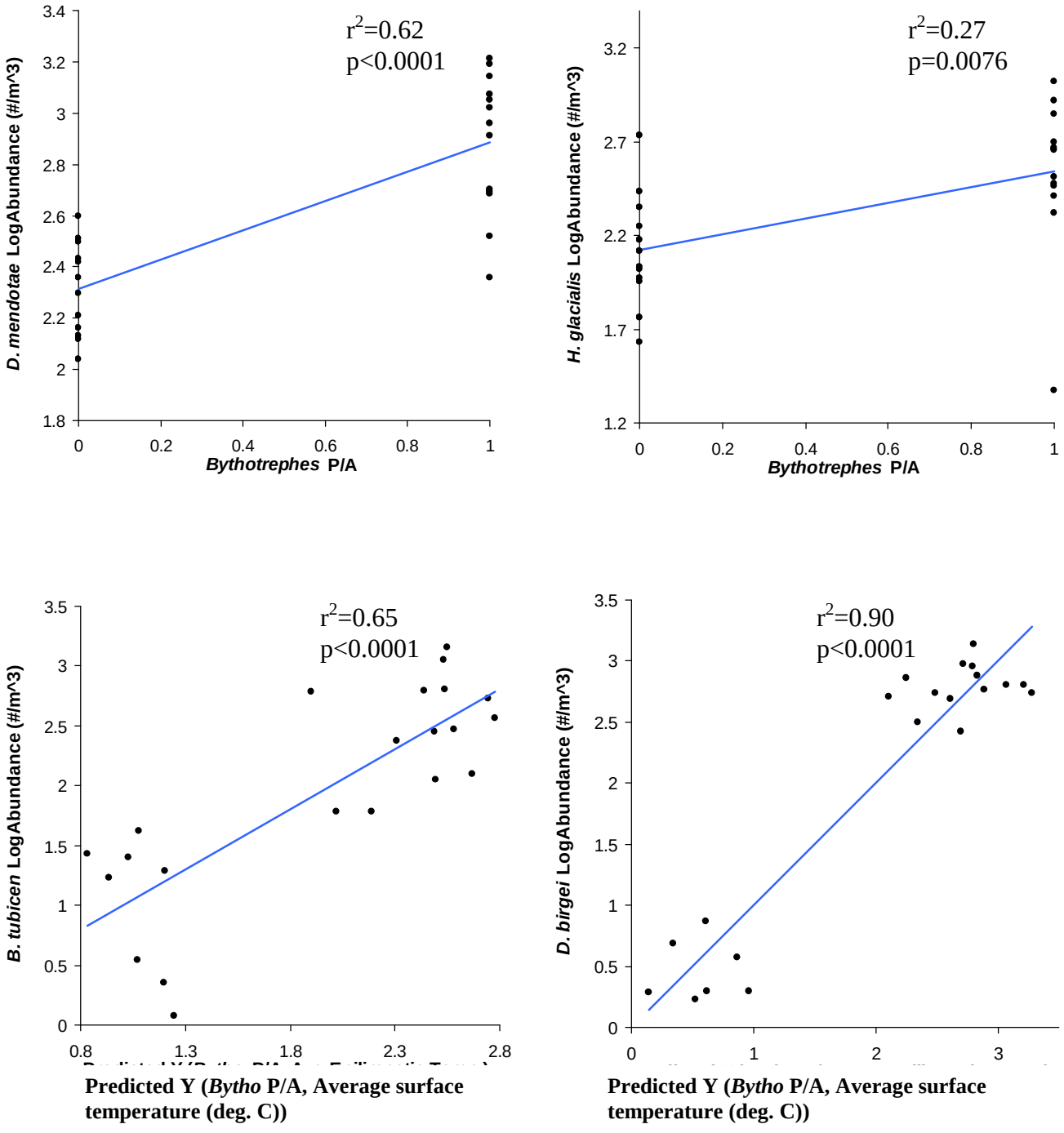


Figure 1.19a: Least squares regression models predicting the average annual abundance of the selected zooplankton species using various scales: *Bythotrephes* (presence/absence), average surface temperature, and days since ice-free.

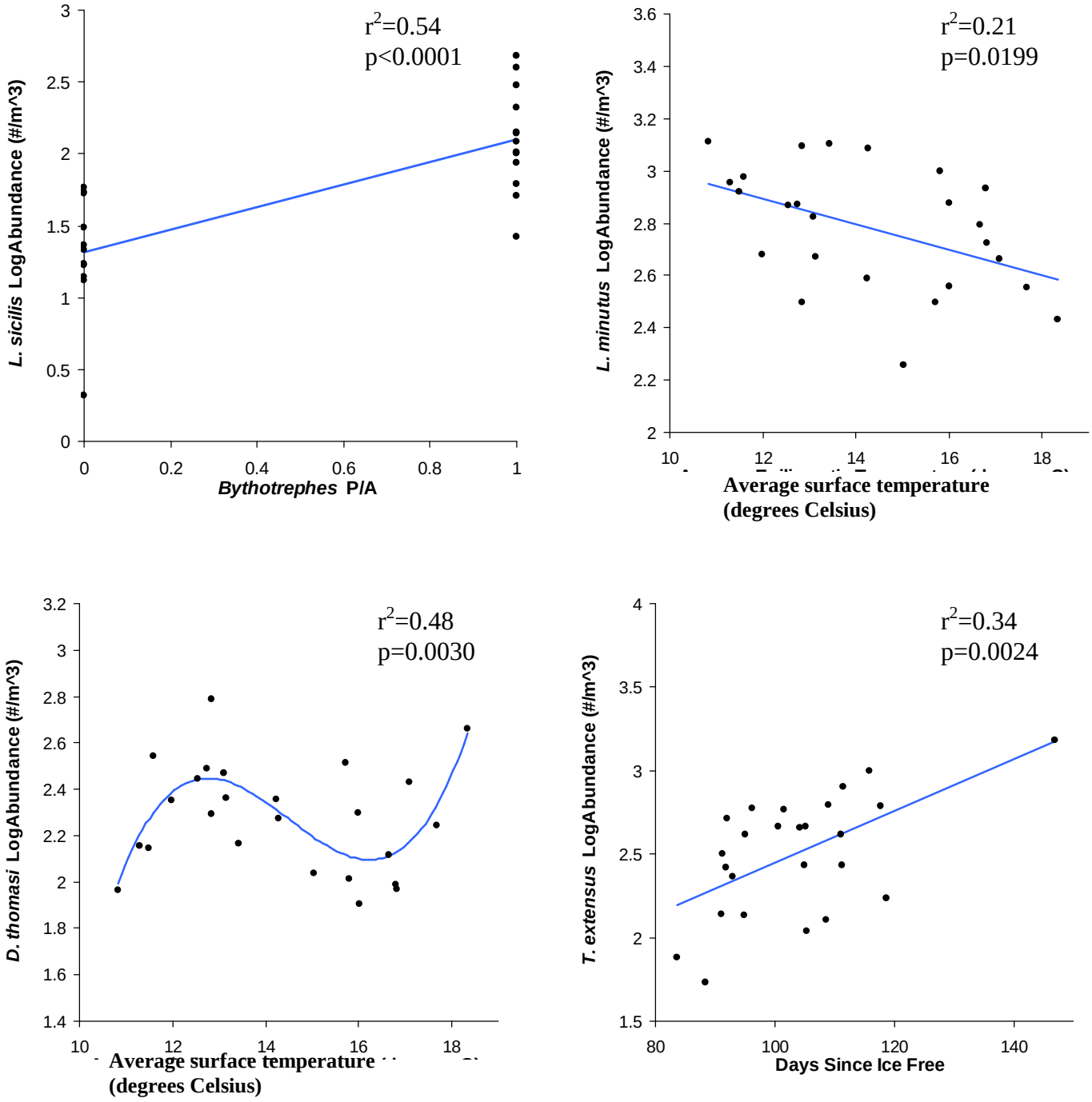


Figure 1.19b: Least squares regression models predicting the average annual abundance of the selected zooplankton species using various scales: *Bythotrephes* (presence/absence), average surface temperature, and days since ice-free.

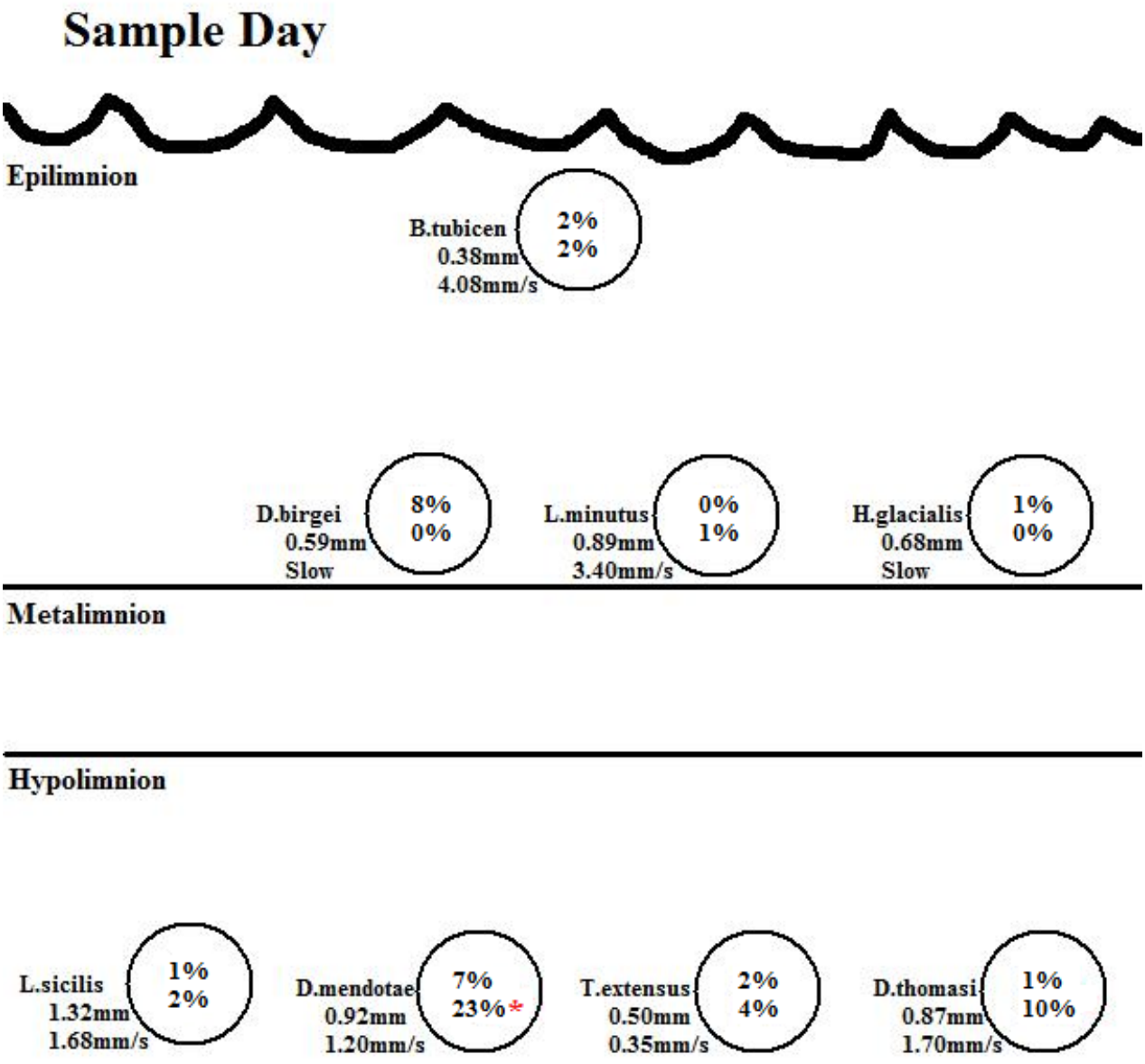
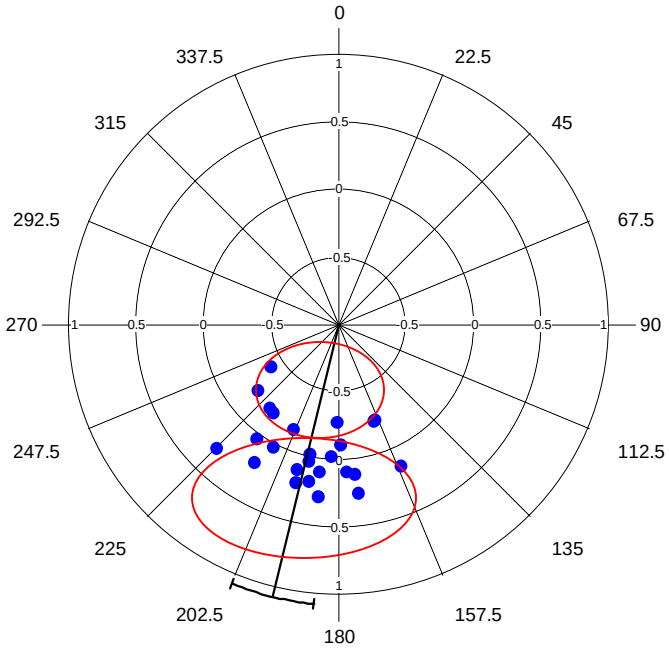


Figure 1.20: A schematic representation of the stratum locations of the selected zooplankton species in Harp Lake. Each circle indicates a specific zooplankton species with the name to the left with the body size and the speed below the name. The 2 values within the circle indicate where the residual abundance is explained by: the wind speed (m/s) (top); wind direction (degrees) (bottom). Asterisk percentage indicates significance ($p<0.05$).

A)



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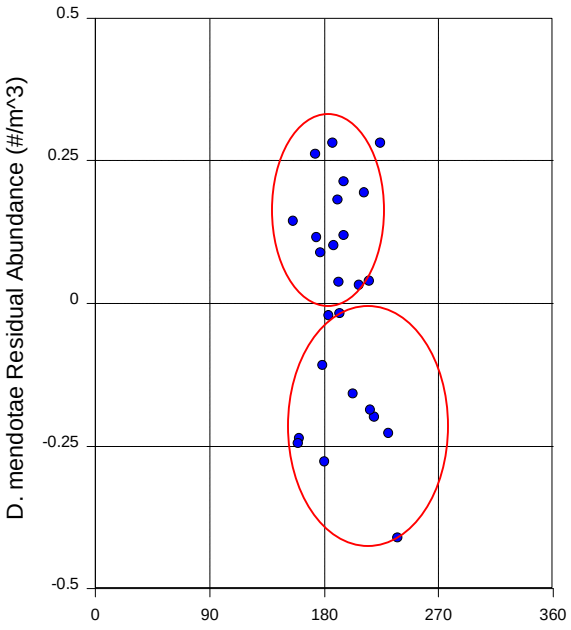

Wind Direction – Sample Day (degrees)

Figure 1.21: Plots demonstrating the association between the residual abundance of *D. thomasi* with wind direction from 1980-2004 over Muskoka Airport. A) Rose plot-scatterplot depiction with a single black arrow denoting the mean wind direction. The top circle indicates the area where the negative residuals complement the wind directions; whereas, the lower circle indicates the area where the positive residuals show a different range of wind directions. B) Two-sample linear-scatterplot. The positive residuals are denoted by the top circle and the negative residuals are denoted by the bottom circle. All plots were generated using Oriana 4.0.

Chapter 2:
Can the prediction of seasonal and long-term zooplankton abundance in Harp Lake be improved using the wind field at daily steps?

Abstract

The predictability of zooplankton abundance under wind-driven currents has been explored, but what has not been explored is how the distributions change over the long-term in response to changes in wind fields. In this study, I sought relationships between the wind field and fortnightly abundances of 8 zooplankton species at a mid-lake station in Harp Lake, Ontario from 1980 to 2004. Over this time period, average wind speed has declined by 25%, which is consistent with the long-term trends over the Northern Hemisphere (Vautard et al. 2010), while direction has shifted 21 degrees towards the north. Multiple linear regressions were generated to predict seasonal and interannual changes in daily zooplankton abundance combining year, Julian day, chemistry and, finally, wind speed and direction. Wind field metrics were included in the models for 6 of the 8 species, although improvements in predictive power were modest. We suspect that the decrease in wind speed has contributed to a change in zooplankton heterogeneity in the lake, and thus a change in lake-wide abundance estimates derived from a single station. Zooplankton are patchily distributed, but most long-term monitoring programs sample only at one station. My work suggests that we may well be able to correct for some of the bias due to a changing wind field, and make small but significant improvements in the predictability of abundance of zooplankton species if we consider wind as a driver.

Introduction

Zooplankton are rarely included among the list of target study organisms in large-scale environmental assessment programs (e.g., Jeppesen et al. 2011). Major bioassessment programs in Europe (Jeppesen et al. 2011), Canada and the United States have been designed to monitor effects of environmental stressors at large scales (Allen et al. 1999; Hughes et al. 2000; EC 2010). For example, the Canadian Aquatic Biomonitoring Network (CABIN) maintained by Environment Canada is a national program designed to assess the condition and biodiversity of Canadian aquatic biota using nationally standardized protocols for data collection (EC 2010). CABIN recognizes many types of biological indicators as suitable for bioassessment, including invertebrates, macrophytes, algae, zooplankton and fish (EC 2010). However, benthic invertebrates, not zooplankton, are recommended by CABIN as the most useful indicators to assess the health of aquatic ecosystems, mainly because benthic invertebrates are easily collected, are found in streams and lakes, reflect site-specific impacts and respond to a wide range of stressors (EC 2010). Similarly, the Environmental Monitoring and Assessment Program (EMAP-surface waters) supported by the United States Environmental Protection Agency (USEPA) has also recommended approaches for monitoring and assessing the nation's lakes and rivers (Hughes et al. 2000). Unlike CABIN, EMAP does not have a standardized protocol for assessment and monitoring of ecological integrity of waters (Hughes et al. 2000; McDonald 2000). Instead, EMAP develops survey approaches that change dependent on the multiple stressors present in the lake/river in question (Hughes et al. 2000; McDonald 2000).

EMAP methodology and survey protocols are based on various ecological indicators, including water chemistry, physical habitat, periphyton assemblages, sediment community metabolism, benthic macroinvertebrate assemblage, aquatic vertebrate assemblages and fish tissue contaminants (Lazorchak et al. 2000). Despite the vast array of ecological indicators used by EMAP, zooplankton is not found on the list of beneficial indicators that can be used to assess water integrity. In fact, the newly implemented European Water Framework Directive (EU WFD) has also entirely disregarded zooplankton as a biological quality element (BQE) for the assessment of water quality (Jeppesen et al. 2011).

The main reason cited for the exclusion of zooplankton from these national bioassessment programs is their lack of production of useful information (Allen et al. 1999). But in their review, Jeppensen et al (2011) and O'Connor et al. (2000) clearly demonstrate the falsity of this conclusion. Zooplankton respond in predictable ways to many anthropogenic drivers. Still, zooplankton have not appeared to be as useful as other indicators in large scale synoptic surveys designed to choose indicators for biomonitoring (Hughes et al. 2000). I believe this may not be due to the inherent lack of usefulness of zooplankton as biomonitors. Rather I hypothesize it is due to problems with sampling procedures that have been employed in these assessments, and in particular their inadequate reflection of zooplankton distributions in time and space. As reviewed in Chapter 1, a single sampling visit to a single station (Allen et al. 1999), cannot fully capture zooplankton distribution nor dynamics. Therefore, I believe that zooplankton communities have yet to be given a fair chance to be recognized as providing beneficial

biological indictors in national and international biomonitoring programs. Research projects involving zooplankton distributions and dynamics need to embrace the 'multiple driving forces' hypothesis of zooplankton distributions in order to reflect ecosystem dynamics (Pinel-Alloul and Ghadouani 2007). This particular hypothesis states that plankton distribution patterns are driven by many processes that include biotic and abiotic elements, including both anthropogenic and meteorological factors (Pinel-Alloul and Ghadouani 2007). Many aquatic ecologists acknowledge that there are many chemical and physical processes that influence plankton distributions, and suggest caution be exercised in the absence of any of these elements when interpreting or exploiting their results (Frank and Leggett 1982; Cloern et al. 1992; Romare et al. 2005; Pinel-Alloul and Ghadouani 2007; Gulati et al. 2008). For example, Allen et al. (1999) found that zooplankton abundance did not significantly correlate with broader-scale factors, e.g., climate change. Not surprising, Allen et al. (1999) collected zooplankton samples from a single vertical net tow. As they sampled at only 1 station, I suggest that inadequate sampling may explain why Allen et al. (1999) failed to detect a climate signal in their zooplankton data. In addition to sampling issues, changes in water mass movements linked to the large local reduction in wind speed, may also have influenced their detection and therefore their possible response.

It is well known that wind influences zooplankton distributions, but it has rarely been evaluated as a predictor of zooplankton abundance in long-term data sets (Sollberger and Paulson 1991; MacKenzie and Leggett 1991; Pinel-Alloul and Ghadouani 2007). Winds move surface waters and thereby affect the distribution of

seston, including zooplankton. If zooplankton are sampled at 1 station, the method used in many bioassessment programs, there is no chance of capturing the spatial dynamics of zooplankton populations. If the wind field changes over year, single-station programs may produce not only inaccurate but also biased results, which may be a consequence of sampling error and inaccurate portrayals of zooplankton dynamics.

In Chapter 1, I showed that changes in the wind field over Harp Lake between 1980 and 2003 did not improve the prediction of the abundance of zooplankton populations at annual steps. However, it remains quite possible that the wind may influence zooplankton abundance at shorter yearly scales (Yan 1986), a possibility best tested by examining correlations between daily abundance and the wind field on actual sampling day or the preceding few days. Here I explore this possibility, again using Harp Lake. Knowing that the Harp Lake community has changed annually in response to the *Bythotrephes* invasion (Yan et al 2001), I model the daily abundance of zooplankton species using first year (that also accounts for the *Bythotrephes* effect in addition to long-term wind effects), and day of year (to account for the known seasonal dynamics of zooplankton in north temperate lakes). Starting by modelling these long- and shorter term known temporal effects, I can then determine if any residual variance may be linked to the wind. I hypothesize that animals found deeper in the water column should be affected less by the wind than epilimnetic taxa, since the wind-induced currents and turbulence decline with depth (Rothschild and Osborn 1988). Thus *D. mendotae* and *L. sicilis* that are deeper in the water column during the day (Young and Yan 2008) should have residual abundance that is negatively correlated with wind because under less water

mixing or lower wind speeds, animals should be able to hold their position or that heterogeneity increased and as a result of sampling at one station, animals may have been missed.

Wind affects currents that are already in motion. Fast and slow wind speeds can move animals or allow animals to move themselves. A negative relationship between abundance and the predictor wind speed result in more animals at low wind speeds and vice versa (Figure 2.1). When there is a positive relationship between abundance and the predictor wind speed, animals are less abundant at low wind speeds (appear patchy, Figure 2.2 – low wind speeds), while at high wind speeds, animals are more abundant (homogeneously distributed Figure 2.2 – high wind speeds). Without the influence of wind on the motion of already moving currents, animals may still be heterogeneously or homogeneously distributed in the water. In the first case, we have fast animals that can appear patchy or heterogeneously distributed since they are able to withstand the strength of the current (Figure 2.3, case 1). In the second case, slow animals are homogeneously distributed in the water because they are not able to withstand the current (Figure 2.3, case 2).

To detect any effect of wind, we must first consider both the long-term and seasonal correlations with zooplankton abundance, but it is also possible that zooplankton are responding to changes in chemistry. As mentioned in Chapter 1, Ca, TP, and SO_4 are decreasing and pH and NaCl are increasing in Harp Lake (Yan and Pawson 1997). To correct for any effect of changes in water quality on zooplankton abundance, I examined 17 water chemistry variables that were assessed in Harp Lake from 1980 to 2004 on the

dates and at the same station that zooplankton were also collected by the DESC crew. Most of these variables have changed over the last few decades with over 50% of the variables increasing while 35% have decreased and the remaining 15% are relatively stable (Palmer et al. 2011). Despite all the published work showing long-term changes in zooplankton in Harp Lake (Yan et al. 2001, Yan et al. 2008), there is still unexplained variance, which may be attributable to the wind. My purpose was to discern if seasonal and annual changes in abundance of zooplankton populations determined at the one mid-lake station in Harp Lake could be better predicted when considering the effect of wind in addition to year, day of year, and water chemistry. I approached this objective by: (1) identifying the variation in the long-term data that could be attributable to year and day of year, i.e. long-term changes presumably attributable to the *Bythotrephes* invasion and to normal phenological patterns (Yan and Pawson 1997), (2) correlating the remaining variation in daily abundance with the wind field on the day of sampling and up to two days before sampling, and (3) determining if short-term wind effects contributed significantly to multiple linear regression models predicting daily zooplankton abundance after variance attributable to year, day of year and water chemistry were considered. Harp Lake served as an optimal site for this work given its many years of fortnightly zooplankton data, with modest changes in water chemistry (Yan et al. 2008), and a well understood change in zooplanktivory from the invading *Bythotrephes* (Yan et al. 2001).

Methods

Harp Lake is a small dimictic lake (71.4 ha) that is located at 45°23'N and 79°07'W. It has a mean depth of 13.3 m and a maximum depth of 37.5 m (Yan and Pawson 1997). This Canadian Shield lake is monitored by the Ontario Ministry of Environment's Dorset Environmental Science Centre (MOE's DESC). The lake has 6 inflows and 1 outflow to the Northeast.

The chemistry of Harp Lake has changed between 1980 and 2004 (Arnott et al. 1999; Molot and Dillon 2008; Paterson 2008; Yan et al. 2008). Ca has slightly decreased from 3.02 to 2.87 mg/L (Molot and Dillon 2008; Yan et al. 2008), while total phosphorus (TP) and dissolved organic carbon (DOC) have declined from 9.02 to 6.35 μg/L and 4.02 to 3.47 mg/L, respectively (Yan et al. 2008). Conductivity, Fe, K, Mg and SO_4 have also decreased modestly (Molot and Dillon 2008). Other parameters have increased, for example Na (0.84 to 1.37 mg/L) and Cl (0.79 to 2.7 mg/L) from the de-icing of nearby roads (Molot and Dillon 2008). There have been both increases and decreases in the abundances of zooplankton species at annual steps (Yan and Pawson 1997; Yan et al. 2002; Yan et al. 2008; Young and Yan 2008), attributed mainly to the 1993 invasion by the non-indigenous zooplanktivore *Bythotrephes* (Yan et al. 2001). The abundances of smaller, less efficient grazers declined, while larger zooplankton (e.g., *D. mendotae*) increased.

Zooplankton were collected biweekly in a series of vertical net tows (from 6m, 6m, 13m, 21m and 30m) that are subsequently combined to produce a bathymetrically-weighted composite at a single station at the deepest portion of the lake during the ice-

free season. The net is138.43 cm long, and 12.4 cm in diameter and is constructed of 76 um mesh (Girard et al. 2007). Sample volumes were calculated from the measured net filtration efficiency (Girard et al. 2007). A minimum of 250 animals were counted and identified in each sample, with subsample volumes adjusted so that no one species or copepodid life stage represented more than 20% of the total count (Girard et al. 2007). All raw data for zooplankton abundance and chemistry can be found in Appendix 5.

As explained in Chapter 1, Harp Lake has experienced changes in the wind field over the study period assuming that data taken from Muskoka Airport can be applied to the lake. At the Muskoka Airport, wind speed has decreased by 25% (4.0 to 3.0 m/s) while the wind direction has shifted more to the North from the Northeast (33 degrees to 12 degrees). The decrease in wind speed is consistent with the Northern Hemisphere atmospheric declines observed from an analysis of 822 surface weather stations between 1979-2008 (Vautard et al 2010). Vautard et al. (2010) suggests that the reason for the changes in the wind field is partially due to a change in surface roughness due to changes in land use.

Zooplankton And Wind Data

I used 1980-2004 zooplankton data from Harp Lake (Yan and Strus 1980; Yan and Pawson 1997; Yan et al. 2008). I used the same zooplankton species as in Chapter 1, selecting common species that differed in physical and behavioural characteristics. All ages of cladocerans were used in this study; however, only adult copepods were used because the immatures were not identified to species. I expected within-year model fits to reflect the omission of the immature copepods for some species, a trend I hoped to

capture with polynomial regression since this method omits predictors that do not significantly contribute to the model.

Wind data were taken from the National Climate Data and Information Archives. George and Edwards (1976) suggested that the distribution of plankton in a shallow reservoir, Eglwys Nynydd, could be influenced by wind data from the previous day, and Petruniak (2009) indicated that the distribution of *Bythotrephes* in Harp Lake was best explained by considering the previous two days of wind data. Therefore, hourly data from the sampling day, and for 1 and 2 days prior to the sampling day were tabulated, and daily means were calculated as simple averages of all hourly data for the respective day. As in chapter 1, I used the wind data from the Muskoka Airport, since the Harp Lake anemometer was affected by forest growth around the MET station (refer to Chapter 1, page 25).

Statistical Analyses

Objective 1: Can the variation in daily zooplankton abundance be explained by year and day of year from 1980 to 2004?

Abundance of the 8 chosen species was available from 1980 to 2004 in Harp Lake over the 291 sampling dates (sample size), where each data series had occasional blanks (Table 2.1). These blanks or "missing data" were replaced with the detection limit for the count on the sample date, e.g., the abundance that would have been reported if 1 animal had been identified in the largest sub-sample counted. An explanation of how the blanks were treated can be found in Appendix 1. Refer to Table 2.2 for a summary of the annual averaged abundance trends in Harp Lake after the missing data were replaced with the

lowest detection limits. There were significant changes in 6 of the 8 species over year. *H. glacialis* and *D. thomasi* did not show any significant trends in abundance over year using linear regression.

In order to determine annual and seasonal contributions to abundance, multiple linear regression models were used. Based on the works of Kleinbaum et al. (1988) and Birkes and Dodge (1993), I generated the best statistical model that helped explain the most variation in abundance with respect to the year and day of year. As the dependent variable I used log-transformed abundances, including detection limit values replacing missing values, of each of the species. Independent variables were: year (nominal scale: 1-25)(Yr), day of year (Julian day)(DOY), Yr^2 to Yr^5, DOY^2 to DOY^5, YrxDOY, and $(YrxDOY)^2$. Polynomial orders up to 5 were used because the model that was best fit was based on the AIC values, which indicated that some models were best at an order of 5. The Analyse-it add-on for Excel (AI) (Analyse-it Software, Ltd. 2011) and Palaeontological Statistics (PAST) (Hammer et al. 2010) were utilized for the model generation. Two programs were used because each provided its own unique contribution to the computation of the models: AI (Analyse-it Software, Ltd. 2011) gave a graphical output of the model and the generated residuals, while PAST (Hammer et al. 2010) gave a value for the AIC. The r^2, F-stat, t-stat and residual assumptions (normal distribution, independence (sum=0)) were the criteria used to assess the fitness of the models. AIC was used to corroborate the fitness of the models and to finalize the choice of the model. VIF values were not used in these computations because a majority of the models derived had polynomial terms and would therefore score very high for multi-collinearity.

Objective 2: Can the remaining variation in abundance be correlated/associated with the wind field?

The residual abundances from the regression models (or from the long-term mean abundance if no regression models were produced) were correlated with the wind speed using Spearman correlations (r_s), and with the wind direction using Pearson correlations (r). All correlations were evaluated at $p = 0.05$. The wind data that were correlated with the residual abundance were the daily average of hourly readings on the sampling date, and one and 2 days prior to the sampling date. I analysed the daily averages on the three days as opposed to taking the 1,2 and 3 day averages in order to better isolate the change in abundance with respect to a particular wind day. AI (Analyse-it Software, Ltd. 2011) was used for the correlations with wind speed, while Oriana 4.0 (Kovach Computing Services 2010) was used for wind direction. The correlations between the residual abundance and wind direction were generated using bivariate linear-circular associations that output a Pearson r-value with an associated p-value. (See equation 1.3 for these calculations and Appendix 2 for how to identify an association between the residuals and the wind direction). A separate Appendix was included in order to interpret the associations because more data (daily data) were used rather than just annual averaged values between 1980-2004. Refer to Appendix 3 for these associations.

Objective 3: Can zooplankton abundance be predicted by year, day of year, chemistry and wind, in Harp Lake?

I began by ranking the 17 chemistry variables to eliminate the influence of scale and to standarize them. I used the principal component analysis routine in PAST (Hammer et al. 2010) to summarize the co-variance of the 17 variables into a smaller

number of orthogonal components. I used the scree plot in PAST (Hammer et al. 2010) to determine how many principal components to include. The first 2 principal components had the greatest variation explained among the chemistry variables according to the scree plot; however, I used 5 principal components in the regression to predict daily zooplankton abundance because the explained variation stabilized after 5 principal components in the scree plot, which may indicate that 5 components are potentially important.

I constructed various multiple linear regression models to determine if the abundance of each species could be predicted by: seasonality and long-term change (year/day of year) alone; water chemistry (chemistry) alone; the wind field alone; year/day of year and chemistry combined; year/day of year and wind combined; chemistry and wind combined; and year/day of year, chemistry and wind combined. I used stepwise regression for the more complex models because I wanted to estimate the contribution of each predictor to the r^2 value for the model. All other models in this study were constructed by fitting the best model using the t-stat and F-stat for the entire model. I did this because the purpose of these models was to analyze the masking effect between predictors.

I used the residual abundance generated from the year/day of year and chemistry models in order to determine if the remaining variation in abundance for all chosen species correlated with the wind field. I did this to evaluate the additional explanatory power of wind on abundance based on models that corrected for year/day of year alone

(Objective 1 and 2) and those that corrected for year/day of year and chemistry (Objective 3).

In the year/day of year, chemistry and wind MLR models, I forced a wind parameter to help predict abundance over year/day of year and water chemistry (ranked PCs). The goal was to obtain a model that had the greatest number of significant predictors that also included the wind field. Those models that did not add a wind parameter were rejected.

To examine the adequacy of the stepwise multiple linear regression (MLR) model, I generated a criterion flow chart that would assist me in choosing the best model (Figure 2.4). To choose the best regression models in AI, I first eliminated predictor terms that were not significant (defined by the t-stat and p-value). Adequate models adhered to the following criteria: they had the lowest AIC values, their Variance Inflation Factor (VIF) suggested little multi-collinearity, the residuals were normally distributed, the F-stat for the whole model was significant, the t-stat for each predictor was significant, the r^2 value was as high as it could be given satisfaction of the previous criteria. In each case where a draft model was rejected, the regression was re-fit and re-tested with the new terms. It is important to note that any models generated without a wind factor were omitted, and the regression was re-run. For instance, if DOY, PC1 and PC2 were included in the model, but no wind factor was included, I continued the search for models that might include the wind. I admit this decision is unusual; however, the rationale of this study was to determine if zooplankton ecologists were in error by never considering the wind in models designed to predict long-term changes in zooplankton

abundance. I chose to give wind every chance to enter the models, as long as it did explain a significant component of the variance, and of course, I could compare these models with the earlier models I generated which included only year/day of year and chemistry. In other words, I wanted to test wind effects.

A problem with stepwise regression is that the larger, more complex model that I started with included terms that may not necessarily have added a significant contribution to the model but still increased the r^2. I dealt with this issue by monitoring the significance of the t-stat for each predictor included in each draft model. To begin the model choice process, predictors with a t-stat with $p<0.20$ were sequentially included to avoid missing terms that might become significant in the final model. I used a p-value of 0.20 after numerous trials because this was the highest p-to-include that resulted in eventual inclusion of predictors in the final model.

When multi-collinearity was an issue, indicated by a high VIF, a compromise was sought between the predictor's unique contribution to the model and the magnitude of multi-collinearity. The VIF values were generated in SYSTAT SigmaStat because AI or PAST did not provide them. The model itself was not disregarded if the VIF values were high because even though the r^2 value may be inflated, there is still a possible chance that the inflated r^2 may still result in a significant model.

Those species that had residual abundance that correlated with a particular wind parameter (speed and/or direction) were considered as potential species that may have wind as a predictor within the MLR models. It was anticipated that any

correlations/associations between the residual abundance and the wind speed and direction would lead to the inclusion of wind variables in the MLR models.

Results

Objective 1: Can the variation in long-term abundance be explained by year and day of year?

The long-term abundances of all 8 species varied between 1980-2004 in Harp Lake (Table 2.2, Figure 2.5-2.7). The abundances of *B. tubicen* and *D. birgei* decreased with year/day of year by 2 orders of magnitude, while *D. mendotae* and *L. sicilis* abundance increased over the study period. The remaining species stayed relatively stable over the entire study period (with temporary oscillations due to seasonality) (Figure 2.5). The most dramatic changes in abundance occurred around 1993, when *Bythotrephes* was found in Harp Lake. The long-term abundances of the individual species were relatively similar during the pre-*Bythotrephes* period of time (1980-1992) (Figure 2.6). However, in 1993, the zooplankton community exhibited drastic changes to the composition and abundance of species. Both *B. tubicen* and *D. birgei* decreased greatly with the presence of *Bythotrephes*, whereas, larger species such as *D. mendotae* and *L. sicilis* populations increased (Figure 2.7).

Zooplankton abundance for all 8 species varied seasonally (DOY) (Figure 2.8). Of the 8 species, 5 major trends were observed over the seasonal data. The abundance had either: a dome shaped trend with high abundance in the middle of the seasonal period (*D. mendotae* and *D. birgei*), high abundance at the start of the ice-free season and a progressive decrease later on (*L. minutus* and *D. thomasi*), low abundance at the start of

the ice-free season and a progressive increase later in the season (*T. extensus* and *B. tubicen*), low abundance at the start of the ice-free season and continuous decrease later in the season (*H. glacialis*) or abundance that was stable throughout the ice-free season (*L. sicilis*). Considering that there were long-term trends and seasonal differences, which varied with species, it was logical to discern how much of the variance in daily zooplankton abundance could be explained by a combination of these two steps, i.e. year and day of year (DOY).

All species abundance could be explained by a combination of DOY and/or Yr in regression models (Figure 2.9abc, Table 2.3). For Figure 2.9ab, abundance was predicted by a single variable (either DOY or Yr), whereas, Figure 2.9c involved a combination of both DOY and Yr variables. For the species, *B. tubicen* and *D. birgei* abundances were best explained by Yr (Figure 2.9a). These species were the most affected by *Bythotrephes*. Approximately 50% of the species abundance required a polynomial fit or multiple predictive terms to best explain abundance. Two of the 8 species had abundance that could be predicted by a combination of independent terms of Yr and DOY (*D. mendotae* and *T. extensus*) (Figure 2.9c). *H. glacialis* and *L. minutus* are best predicted by DOY (Figure 2.9a). These species were most affected by seasonality with increases and decreases in abundances throughout the seasonal period.

Objective 2: Can the remaining variation in abundance be associated with the wind field?

In 21% of cases, the residual abundance generated from the year/day of year models was significantly correlated with wind speed or direction (Table 2.4). Residual

abundances of *B. tubicen* and *T. extensus* were not correlated with the wind field. In contrast, the residuals of *L. minutus* abundance were correlated with both wind speed and direction (Table 2.4). *L. minutus* residual abundance was correlated with wind speed on the sampling day and on the two previous days. Two of the three metalimnetic species (*L. minutus* and *D. birgei*) had residual abundances that were correlated with wind speed and direction. Refer to Appendix 4 (Figure 4.3 and 4.4) for the plots between residual abundance and wind speed and wind direction, respectively.

Objective 3: Can zooplankton abundance be predicted by year/day of year, chemistry and wind in Harp Lake?

Based on the scree plot generated in PAST, 2 principal components explained the variation among the 17 chemistry variables from Harp Lake (Table 2.5). Principal component 1 (PC 1) explained 39% of the variance in ranked water quality data, and captured to rising Cl and Na and falling SO_4. PC 2 accounted for 21% of the variance and reflected changes in Gran Alkalinity and Mg.

Of the 56 possible models produced (including year/day of year and/or chemistry and/or wind) to explain variation in abundance, 46 models were generated (Table 2.6). As the models became more complex (e.g., year/day of year and chemistry and wind combined), fewer models were possible. All models combined explained 1-60% of the variation in abundance. *D. mendotae*, *H. glacialis* and *L. minutus* abundances were explained by each of the model types (all 7 types), while *T. extensus* had abundance that was least explained (only 3 of the 7 types).

The abundance of each species could be explained by chemistry (PC 1-5) (Table 2.7) with 7-39% of the variation explained. The small cladocerans (*B. tubicen* and *D. birgei*) had the greatest variation in abundance explained by water chemistry (37 and 39%, respectively). Cladoceran abundance was better explained by water chemistry relative to copepod abundance (23.75:6.25%, on average per species). *L. sicilis* was the only species that had abundance explained by PC5.

Significant models were produced using wind alone for 6 species. On average, 8% of the variance was explained. No significant models were found for *D. birgei* and *T. extensus*, (Table 2.8). The variation in abundance that could be explained ranged from 1-8%. The greatest variation in abundance that could be attributable to wind was for *L. minutus* (8%), whereas the least variation explained was for *D. thomasi* (1%). The majority (4 of 6) of models included an interaction term between wind speed and direction (e.g., Spd24*Dir24).

All species had abundance that could be predicted by a combination of year/day of year and chemistry in MLR models, which included, either Yr, DOY, YrxDOY (an interaction term), and/or PC 1-5 (Table 2.9). *D. mendotae* abundance was predicted by year and PC 3 (DIC and TKN) (r^2=0.14, p<0.0001). *H. glacialis* abundance was predicted by day of year and PCs 1 (NaCl, SO_4) and 3 (DIC and TKN) (r^2=0.12, p<0.0001). *B. tubicen* abundance was predicted by day of year, year, day of year and year interaction term, and PCs 1 (NaCl and SO_4), 2 (Gran_Alk and Mg), and 3 (DIC and TKN) (r^2=0.39, p<0.0001). *D. birgei* abundance was predicted by day of year, year, day of year and year interaction term, and PCs 1 (NaCl and SO_4), 2 (Gran_Alk and Mg), and

4 (DOC and TKN) (r^2=0.60, p<0.0001). *L. sicilis* abundance was predicted by day of year and PCs 1 (NaCl and SO_4), 2 (Gran_Alk and Mg), 4 (DOC and TKN) and 5 (DOC and TKN) (r^2=0.11, p<0.0001). *L. minutus* abundance was predicted by day of year, year, day of year and year interaction term, and PC 3 (DIC and TKN) (r^2=0.31, p<0.0001). *D. thomasi* abundance was predicted by day of year, year and PC 3 (DIC and TKN) (r^2=0.15, p<0.0001). And finally, *T. extensus* abundance was predicted by day of year and PC 3 squared (PC 3^2) (DIC and TKN) (r^2=0.19, p<0.0001).

Seven of the 8 species had abundance that could be predicted by seasonality (excluding, *D. mendotae*) in the year/day of year and chemistry MLR models (Table 2.9). The majority of the cladoceran species (3/4) had a positive relationship between abundance and day of year, while the copepods had no particular pattern (slope being 0). Year was included with day of year in 4 species models (*B. tubicen*, *D. birgei*, *L. minutus* and *D. thomasi*). In all these cases, there was a negative relationship between abundance and year.

Six of the 8 species had abundance that could be predicted by PC 3 (DIC and TKN) (excluding, *D. birgei* and *L. sicilis*) in the year/day of year and chemistry MLR models (Table 2.9). In all instances, the relationship between abundance and PC 3 were negative. This indicates that lower abundances were found at high concentrations of DIC and TKN.

The residual abundance generated from the year/day of year and chemistry models had 11 of the 48 (23%) possible cases correlate with the wind field (speed and direction) (Table 2.10). *D. mendotae* and *T. extensus* had the largest correlation between

the wind fields (50% of all possible cases or 3 of the 6). For *B. tubicen* and *L. sicilis*, residual abundance was not explained by the wind field. *T. extensus* had residual abundance that could be significantly explained by all wind speed days (sample day, 24-hours prior to- and 48-hours prior to the sample day). In comparison between the correlations using residual abundance from year/day of year alone and year/day of year and chemistry combined, there were more significant cases found for the latter (2% difference or 10 vs. 11 possible cases). Therefore, after considering the variation in abundance attributable to year/day of year and chemistry, the wind field could still improve the prediction of abundance.

Five of the 8 species had abundance that could be explained by a combination of year and day of year and wind (speed and direction) (excluding *L. sicilis*, *D. thomasi* and *T. extensus*) (Table 2.11). Among those species, the variation in abundance explained ranged between 7-54%. All species with a significant model had abundance explained by DOY. Two of the 3 metalimnetic species had abundance explained by speed on the sample day (SpdS) (*D. birgei* and *L. minutus*). The year/day of year predictor may be masking the variation attributable to the wind field because 3 species abundances could not be explained by both year/day of year and wind combined.

The abundance of 6 of the 8 species was explained by a combination of chemistry and wind field, ranging from 6-40%. All cladocerans had abundances that could be explained by PC3. *D. thomasi* and *T. extensus* abundance could not be explained by a combination of chemistry and wind. In contrast with the chemistry models alone, these

species could be explained by chemistry; therefore it is possible that chemistry is masking the variation attributable to wind.

After acknowledging that wind did explain some of the variation in residual abundance, nine MLR models were generated by forcing a wind variable to predict the abundance. Models were generated for 6 of the 8 species (Table 2.13). *D. mendotae* abundance was predicted using Yr, wind speed 48-hours prior to the sample and wind direction on the sample day (r^2=0.14, p<0.0001). *H. glacialis* abundance was predicted using DOY, PC 3 (DIC and TKN), wind speed and direction 24 hours prior to the sample date and an interaction term for speed and direction 24 hours prior to the sample (Spd24xDir24) (r^2=0.19, p<0.0001). There was multi-collinearity among variables within the *H. glacialis* regression models but these models were not disregarded because the models still had an r^2 value that is significant (VIF values of 7.169, 7.169, and 18.38 for Spd24, Dir24 and Spd24xDir24, respectively). The *D. birgei* model included year, PCs 1 (NaCl and SO_4), 3 (DIC and TKN), and 4 (DOC and TKN), and the wind speed 48 hours prior to the sample (r^2=0.44, p<0.0001). *L. minutus* abundance was predicted using several models: (1) using DOY, PC 2 (Gran_Alk and Mg) and the wind speed on the sample date (r^2=0.09, p<0.0001), (2) using DOY, PC 2 (Gran_Alk, Mg) and the wind speed 48 hours prior to the sample date (r^2=0.11, p<0.0001), (3) using PC 2 (Gran_Alk and Mg) and wind speed 24 hours prior to the sample date (r^2=0.04, p<0.0001), and (4) using PC 2 (Gran_Alk and Mg) and wind direction on the sample date (r^2=0.05, p<0.0001). *L. sicilis* abundance was predicted using wind speed on the sample date with PC 4 (DOC and TKN) (r^2=0.04, p<0.0001). Finally, *D. thomasi* abundance was predicted

using PCs 3 and 4 (DIC, DOC, and TKN) and wind speed 24 hours prior to the sample date (r^2=0.06, p<0.0001). Both *B. tubicen* and *T. extensus* abundance could not be predicted using a model that incorporated a combination of year/day of year, chemistry and wind. These species are the smallest of the 8 species used in this study.

A comparison of the MLR models using year/day of year and chemistry alone and those that included wind, it is apparent that the inclusion of wind did mask some of the predictors that caused patterns in the abundance of the chosen species. Here by masked, I mean the exclusion of a potential predictor that overshadowed the contribution of the wind parameter and is then ignored. Masking is a common problem in linear regression because after the deletion of a term, other terms may become visible and appear modestly influential, as with wind in this case (Lawrence 1995, Nurunnabi et al. 2011). In the MLR models for year/day of year and chemistry, 6 of the 8 species (excluding *B. tubicen* and *T. extensus*) had a year/day of year and/or chemistry predictor masked by the inclusion of the wind parameters. For instance, *D. thomasi* abundance in the MLR models for year/day of year and chemistry was predicted by –DOY, -Yr, and – PC 3, while the model that included wind had abundance predicted by PC 3 in addition to a wind field parameter (Table 2.8). As a result, by including the wind variable, the variation in abundance that was explained by year/day of year was masked by the inclusion of wind, however PC 3 remained and was not hindered by the wind parameter. Another example would be the species *L. sicilis.* I predicted *L. sicilis* abundance using year/day of year and chemistry by multiple predictors: +DOY, +PC 1, -PC 2, -PC 4 and +PC 5 (Table 2.6). However, when a wind field parameter was included to explain *L.*

sicilis abundance, all predictors except –PC 4 were dropped (Table 2.8). Again, the inclusion of wind masked year/day of year and/or chemistry that would usually be included in the models to explain abundance.

When the 9 MLR models were evaluated using individual predictors, the majority of the wind variables explained a significant portion of total variance in the data (Table 2.14a,b). In the case of model 1, *D. mendotae* abundance was predicted by Yr, Spd48 and DirS. Both Spd48 and DirS significantly explained, 1.4 and 1.2% of the variation, respectively (Table 2.14a). In the case of model 4, *L. minutus* abundance was predicted by DOY, PC 2 and SpdS. Actually, SpdS contributed more (3%) to the model than the chemistry variable (PC 2, 2%) (Table 2.14a). However modest the contribution, these MLR models demonstrate that wind does contribute to the prediction of abundance.

Discussion

Wind metrics could be used to improve the prediction of daily zooplankton abundance in Harp Lake in addition to year, day of year and chemistry. Year and/or day of year alone, explained 9-54% of the variance in zooplankton abundance. Chemistry alone, explained 4-39% of the variance on abundance. Using all wind days combined (sample day, and 1 and 2 days before the sample day), both wind speed and direction uniquely explained only 0-2% of the variation in the residual abundance. The combination of year/day of year and chemistry explained 11-60% of the variance in zooplankton abundance. While the combination of year/day of year and wind models explained 7-54% of the variance in abundance. After correcting or modeling abundance

against year/day of year and chemistry, the residual abundance correlated with the wind field in 23% of the total possible cases. Knowing that wind may influence residual abundance, 9 MLR models were generated to explain zooplankton abundance using year/day of year, and/or water chemistry and wind for 6 of the 8 species. Frank and Leggett (1982) used degree-day with wind (wind speed on sample day) to explain zooplankton abundance off the Newfoundland coast. However, the usage of long-term data in order to link the relationship between abundance, year/day of year, water chemistry and wind has never been pursued. The present study suggests that it is worth examining the effects of the wind on zooplankton abundance, but it suggests that the understanding gained will be modest.

As previously mentioned, year/day of year alone explained quite a bit of variation in the abundance of the chosen zooplankton species. *B. tubicen*, *D. birgei* and *L. sicilis* had abundance that was explained only by year (Yr) (49, 37 and 9%, respectively). Both small cladocerans (*B. tubicen* and *D. birgei*), had the greatest percentage explained by year, among these three species. This result is consistent with the presence of *Bythotrephes* in Harp Lake and the decline of both these species after 1993 (Yan and Pawson 1997). Therefore, it was expected that the abundance of these species would reflect a stronger change with year than displaying a trend with seasonality or day of year. Yan and Pawson (1997) also found that *L. sicilis* abundance has increased since the invasion of *Bythotrephes* and this is consistent with the results of this study. *D. mendotae* and *T. extensus* abundance was explained by year (*Bythotrephes* presence) and day of year (seasonality) (54 and 20%, for the species respectively). This result suggests that the

abundance of these species is better explained by a yearly change (such as the presence of *Bythotrephes*) and by seasonal events. For example, *D. mendotae* abundance was predicted by a combination of year and Julian day with low abundance early in the season/year and high abundance later on. However, it is surprising that *T. extensus* showed a significant positive relationship explained by year. According to Yan and Pawson (1997), *T. extensus* was among the species that decreased with the presence of *Bythotrephes* in 1993 hence, I expected abundance would continue to fall over time. However, my study extends beyond 1997 (Yan et al. 2001), and *T. extensus* abundance began to increase after 1999. Why *T. extensus* has recovered from the initial negative impacts of *Bythotrephes* warrants study. This recovery may be due to the largely algal dietary resources of *T. extensus,* particularly the rotifer, *Polyarthra remata* (Dieguez and Gilbert 2002).

Residual abundance generated from the year/day of year models significantly correlated with the wind field (speed and direction) over the region during 1980-2004 for 21% of all possible cases (out of 48: 8 species x 3 wind days x 2 wind field parameters) and explained 0-2% of the variance in the residual abundance. The only species that did not have residual abundance that could be explained to some extent by the wind field were *B. tubicen* and *T. extensus*. This is not surprising because these are the smallest zooplankton species of the 8 (0.038, 0.050 cm, respectively). The small size would allow the animals to be moved around the water column more easily and thereby maintain their homogeneous distribution regardless of their preferred strata (Moreno-Ostos et al. 2009). *B. tubicen* did not significantly correlate with the wind speed. This was unexpected since

this species is capable of quick bursts of 0.408 cm/s (Lagergren et al. 1997). A capacity for such quick bursts may not be enough for the changes in wind speed to lead to changes in their distribution. In addition, *B. tubicen* is the only species chosen that is found in the surface waters during the daytime and would therefore be the most susceptible to the effects of wind as well as predation (Yan et al. 1997). The lowest wind speed (0.47 m/s or 47 cm/s) and thereby, the wind force (~1.5% of the wind speed = 0.705 cm/s) over the surface waters would have been too strong even for maximal bursts performed by this species (0.408 cm/s).

L. minutus had residual abundance that was correlated with wind speed and direction in 4 of the 6 possible cases, including wind speed on the day of sampling and the previous 2 days. These results are not surprising since *L. minutus* is a medium-sized (0.089 cm), fast swimming (0.340 cm/s) metalimnetic species (Dieguez and Gilbert 2002, Muirhead and Sprules 2003). Its location in the water column and size/speed allows this species to resist the current, which is induced by the wind and in most cases (4 of 6) *L. minutus* can maintain its position in the water and withstand turbulence and flow. Imberger and Hamblin (1982) and Gorham and Boyce (1989) have documented that the turbulence, internal waves (baroclinic waves) and heat transfer are dampened at the base of the mixed layer (surface waters) that marks the top of the metalimnion. Since the wind has a dampened effect in the metalimnion, it is reasonable to find the majority of the metalimnetic species to be able to withstand (or have abundance correlated with) the wind field (*L. minutus* and *D. birgei*). *H. glacialis* is the only species in the metalimnion that did not have residual abundance that was significantly correlated with the wind speed

(although 1/3 possible cases for wind direction was significant). This makes sense because *H. glacilais* is known to be very slow, given its gelatinous capsule (Link 1996), and would therefore not be able to resist the wind-induced currents within the metalimnion, even though they are relatively slow.

What does this all say about the importance of the wind on zooplankton abundance? After correcting for year/day of year, residual abundance can be used to explain an additional portion of the variation in zooplankton abundance. Knowing that the wind may explain some variation in zooplankton abundance, it is possible that it is not just a mere coincidence as suggested in Chapter 1 discussion. Therefore, the addition of wind into models, along with year/day of year and other predictors (e.g., anthropogenic factors), may help further illuminate our understanding of zooplankton in their aquatic ecosystems.

Residual abundance remaining from the year/day of year and chemistry models was significantly correlated with the wind field (speed and direction) for 23% of all possible cases (11 of 48 cases) and explained 0-2% of the variance in the residual abundance. The wind field better predicted the residual abundance from the year/day of year and chemistry models compared to the year/day of year models alone (23% vs. 21%; 11 vs. 10 cases). Surprisingly, *T. extensus* had residual abundance that significantly correlated with all wind speed days. This is unexpected because *T. extensus* residual abundance did not correlate with any aspect of the wind field for the year/day of year models alone. This may be a result of the masking of the wind field by chemistry, when explaining the variation in abundance. For instance, the year/day of year models alone

did not incorporate any variation in abundance due to chemistry, however when chemistry was considered a predictor, the variation in abundance due to the wind field became evident. After correcting for year/day of year and chemistry, *T. extensus* abundance could be explained by the wind field.

The majority of the species (5 of the 7) that had residual abundance that could be explained by wind direction on a particular wind day were the same for the year/day of year alone and year/day of year and chemistry models (*D. mendotae*-DirS, *H. glacialis*-Dir24, *D. birgei*-Dir24, *L. minutus*-DirS and *D. thomasi*-DirS). That variation associated water chemistry did not mask the variation in residual abundance explained by wind direction. For instance, *H. glacialis*, *D. birgei* and *D. thomasi* had residual abundance that was explained by wind direction on the same wind days (e.g., Sample day) when corrected for the year/day of year alone models as well as the year/day of year and chemistry models. If water chemistry were masking the variation in abundance attributable to the wind field, the residual abundance of these species would not be correlated with the wind field.

By forcing wind into MLR models in addition to year/day of year and chemistry it appears that some predictors can be masked by the wind (e.g., year or day of year). However, when wind was given a chance (or termed as "forcible inclusion"), nine models were successfully generated to include either year/day of year and/or water chemistry and wind. Each of these models will be discussed below. To simplify the understanding behind the predictor and its relationship with abundance, an overall discussion of the predictors will be organized by: year/day of year, water chemistry with principal

components and finally wind as opposed to discussing each model. However, it is important to note that each model was derived individually. When discussing the models and the relationship between abundance and a predictor, the annual averaged Harp Lake water chemistry or abundance information can be found in Tables 2.2 and 2.15.

Wind did not load into any MLR models to predict the abundance of *B. tubicen* or *T. extensus*. This is not surprising considering that their residual abundance after correcting for year/day of year did not correlate with the wind field (note: only models that contained a wind field predictor were chosen). Both these species are very small. *B. tubicen* is capable of fast bursts but resides in the epilimnion, which is more exposed to the wind (George and Edwards 1976). However, it is surprising that *T. extensus* did not show a predictive relationship between abundance and the wind field because it resides in the hypolimnion (Barbiero et al. 2005). Those species lower in the water column are less susceptible to wind-induced currents and could therefore potentially withstand any effect of changes in the wind. This difference in current versus swim speed may be the reasoning behind the inability of *T. extensus* to withstand any currents and therefore be homogeneously distributed over spatial and temporal scales. Small zooplankton species that are either too slow to overcome the current or too close to the surface waters (mixing layer) are potentially important species that may be used in bioassessment programs with confidence that any changes in wind will not confound interpretation of their abundance data.

Year and day of year were important variables that were included in the models of 4 of the 6 remaining species. To start, the presence of *Bythotrephes* in 1993 in Harp Lake

caused zooplankton to either out swim this invader or that the animal was large enough to compete for resources amongst other conspecifics. Yan and Pawson (1997) found that larger cladocerans increased in number after the appearance of *Bythotrephes* and that smaller species declined. Therefore, it is expected that the large cladoceran *D. mendotae* would prevail in the presence of *Bythotrephes* and smaller species such as *D. birgei* would decline. However, Schulz and Yurista (1995) found that *Bythotrephes* actually preferred larger daphniids, such as *D. mendotae*, therefore *D. mendotae* body size would not be a likely reason for its success over time. Also, *D. mendotae* is known to avoid *Bythotrephes* (Pichlova-Ptacnikova and Vanderploeg 2011) and is most likely the reason why *D. mendotae* increased with year in Harp Lake. Therefore using year in order to better explain species that have increased or decreased would be important when predicting their future abundance in Harp Lake.

H. glacialis and *L. minutus* both were negatively associated with day of year. *H. glacialis* abundance rose for the first 50 days and then fell gradually thereafter. In particular, cladocerans are known to have thermal limits and they are unable to live at temperatures as high as 30 degrees (Throp and Covich 2010). These animals are more adapted to cooler temperatures, therefore as the summer progresses (or day of year), the temperature increases and the animals begin to decline or the spring food production is over and the resources are limited (Throp and Covich 2010). These increases in temperature are especially important since the climate is continuously warming, which is also observed in Harp Lake surface waters. At 1 m depth, the average surface temperature is increasing with year (refer to Chapter 1, page 67). This may explain why

there is a negative relationship between *H. glacialis* abundance and day of year. It is also possible that the gradual decline in abundance over the summer may be food related. They have a burst of production in the spring associated with the spring algal bloom and then limp along the rest of the year (Throp and Covich 2010). In the case of *L. minutus*, the negative association between abundance and day of year is an artefact of the MOE's sample counting and the life history of this species. Calanoids have 6 naupliar and 6 copepodid life stages (Throp and Covich 2010). Adults only were identified to species in this study while immatures were counted but not identified to species. Therefore I could not include immature life stages in the models. The addition of these life stages may have increased the abundance estimate of *L. minutus* during the ice-free season and changed its relationship with DOY. In summary, both year and DOY can be useful predictors of daily abundance of zooplankton.

Excluding *D. mendotae*, all species with successful MLR models included chemistry, i.e. PC1, 2, 3 and/or 4. PC1 mainly summarized changes in NaCl and SO_4, and loaded into the model for *D. birgei* abundance. High salinities (e.g., 30 psu), do impact the reproductive life stages of *Diaphanosoma*. For example, the life span of *D. birgei* decreased from 24 days to 5 days at higher salinities (5, 17, 25 and 30 psu, Achuthankutty et al. 2000). Ca is known to influence the sensitivity of zooplankton to salt (Rahaman 2006); however Achuthankutty et al. (2000) did not evaluate salinity with respect to Ca levels. At the present time, the salinity in Harp Lake is increasing due to the de-icing of winter roads that surround the lake (Yan et al 2008). However, the salinity in Harp Lake is still far from the extreme levels of the salinity tested in

Achuthankutty et al. (2000) (Harp Lake average salinity ~0.00356 psu, 1000 times lower than damaging thresholds). Therefore, based on the low levels of NaCl in Harp Lake, I propose that salinity is not directly affecting *Diaphanosoma* abundance. Nevertheless, after correcting for the *Bythotrephes* effect using year, the negative relationship between *D. birgei* abundance and PC1 is still present and therefore even a small amount of NaCl may be affecting *D. birgei* abundance.

As the next constituent of PC1, SO_4 levels in Harp Lake are decreasing as SO_2 emissions in eastern North America fall, yet sulphate is not toxic. Therefore the link between SO_4 and abundance is not causal. *D. birgei* has been found in waters with SO_4 levels much higher than those in Harp Lake (up to 24.5 mg/L in Northern lakes) (Keller and Pitblado 1989). Pinel-Alloul et al. (1990) also observed a positive correlation (r=0.40) of *Diaphanosoma* with SO_4 in Quebec lakes. Since SO_4 is decreasing in Harp Lake, there is a positive relationship for *D. birgei*. Therefore, the link between SO_4 and *D. birgei* abundance is not apparent.

L. minutus was the only species that had PC2 (explained by Gran_Alk and Mg) included in the MLR models. This is not surprising since *L. minutus* dominates in waters that have high alkalinity (e.g., 191 mg/L as $CaCO_3$, Shaw and Kelso 1992). In fact the levels of alkalinity are increasing in Harp Lake, i.e. with higher alkalinity, more *L. minutus*. PC2 is also correlated with Mg, which is decreasing in Harp Lake from 1.02 mg/L to levels as low as 0.80 mg/L, however modest. According to Keller and Pitblado (1989), *L. minutus* can dominate waters that have Mg levels as high as 15 mg/L.

Therefore it is unlikely that the link between *L. minutus* and Mg is a cause/effect relationship.

PCs 3 and 4, associated with inorganic and organic carbon and TKN were included in models for *D. birgei*, *H. glacialis*, *L. sicilis* and *D. thomasi*. All these species had abundance that increased with TKN and DOC, and decreased with DIC (PC3). In Harp Lake, DOC and TKN are positively correlated ($r_s=0.19$, $p<0.0001$), therefore I must discuss them jointly. Both *D. birgei* and *H. glacialis* were more abundant when TKN levels were low to moderate (110-1120 µg/L vs. >2300 µg/L) (Keller and Pitblado 1989). Keller and Pitblado (1989) reported that in northern Ontario lakes, 82-84% of *Diaphanosoma* were found in lakes where TKN levels were between 110-1120 µg/L and only 48% of the lakes contained this species when TKN peaked at 2300 µg/L. Likewise, 71-90% of the *H. glacialis* were also found at low TKN levels, with only 42% of higher-TKN lakes containing this species (Keller and Pitblado 1989). In the study by Keller and Pitblado (1989), *D. thomasi* abundance was present in almost all the lakes (86-94%) at all ranges of TKN. In Harp Lake, the highest level of TKN was 261 µg/L and higher abundances were found at lower TKN levels.

Four of the 8 zooplankton species had a negative correlation between abundance and DIC/DOC in the MLR models (*H. glacialis, D. birgei, L. sicilis* and *D. thomasi*). A possible reason for this negative relationship could be related to strata location. All these species are found lower in the water column, below the epilimnion where DIC/DOC levels are higher (Kamjunke et al. 2004). *H. glacialis* and *D. birgei* are found in the metalimnion during the day (Tessier 1983, Doulka and Kebayias 2008), while *L. sicilis*

and *D. thomasi* are found in the hypolimnion (Barbiero et al. 2005, Young and Yan 2008). Those species that inhabit the metalimnion are subjected to dampened turbulence from wind-induced currents and thereby less turbidity, which leads to increased levels of particulate matter (and higher DIC/DOC levels). Unlike the metalimnetic species, *D. thomasi* particularly thrives in deep, clear waters where turbidity is at its lowest (Balcer et al. 1984, Lytle and Snoeyink 2003). In fact, *D. thomasi* has been found to negatively correlate with the turbidity of water (r=-0.30) (Pinel-Alloul et al 1990). It is understandable that metalimnetic and hypolimnetic species that reside below the epilmnion would be negatively associated with DIC/DOC, since levels are found to be higher below the surface waters (Kamjunke et al. 2004). Therefore, when studying zooplankton, using DIC/DOC and TKN as predictors to estimate abundance would be worthy of study since zooplankton respond to levels dependent upon their location in the water.

Both wind speed and direction were forcibly included as predictors that explained zooplankton abundance. The prediction of abundance of 6 of the 8 species could be improved by the inclusion of a wind parameter within a MLR model in addition to year/day of year and/or water chemistry. Wind speed was a better predictor than wind direction. Wind direction on the sample day was included as a predictor for 2 of the species (*D. mendotae* and *L. minutus*), whereas wind speed was included in the models of all the species. The abundances of *D. mendotae*, *D. birgei* and *L. sicilis* were negatively correlated with wind speed on the sample date or 48 hours prior to sampling. The wind effect (which was significant) for each of these species was 2, 2 and 1%, respectively.

This negative relationship indicates that animals are more abundant at lower wind speeds and fewer animals are present at higher wind speeds (Figure 2.1). This may indicate that animals can hold their position in the water under low wind-induced mixing. Under high wind mixing, animals may become transported elsewhere in the water column (upwelled or downwelled, depending on their original strata location). For instance, *D. mendotae* abundance was negatively associated with wind speed 48 hours prior to the sample taken. Since this species is found in the hypolimnion (Young and Yan 2008), low wind speeds would cause slower currents in the surface waters that cannot penetrate through the metalimnion (Heaps and Ramsbottom 1966) and therefore, the internal wave movements of the hypolimnion cease or weaken. At higher wind speeds or more turbulent waters, there is a better chance that the hypolimnion is oscillated back and forth with a frequency of the internal wave period (Antenucci and Imberger 2003). The internal wave period in Harp Lake was 160 minutes in the summer of 2007 (Petruniak 2009). This means the thermocline tilts back and forth from one end of the lake to the other approximately every 3 hours. In a 48-hour period, the internal wave at the metalimnion would have oscillated 16 times. This oscillation causes animals in the water to become transported upwind or downwind depending on their location in the water. For *D. mendotae*, the high wind speeds cause the movement of the internal wave at the metalimnion and animals are transported downwind and upwelled, unless they are able to resist being pushed upward (Waife and Frid 1996) (Figure 2.1). This is the same case with *L. sicilis* (except this species is always hypolimnetic), however abundance was negatively associated with the wind speed on the sample day. *D. birgei* is found in the metalimnion (Doulka and

Kebayias 2008), where the water movement is dampened due to the temperature gradient and therefore results in decreased turbulence (Elci 2008). Therefore, both the metalimnion and hypolimnion experience a similar amount of wind-induced turbulence and animals found within those strata would react similarly to the wind speeds.

H. glacialis, *L. minutus* and *D. thomasi* had abundance that positively correlated with the wind speed on either the sample date, 24-hours prior to- and/or 48-hours prior to the sample being taken (variance explained for the wind variable: 2, 4 and 1 %, respectively). This positive relationship indicates that animals were less abundant at lower wind speeds and more abundant, earlier in the records, when wind speeds were higher (Figure 2.2). This may indicate that animals cannot hold their position in the water under high wind speeds because the wind is too strong and is penetrating through to the metalimnion (Colebrook 1960). Under lower wind speeds, animals are able to hold their position in the water and become patchy (heterogeneously distributed) (Rinke et al. 2007). Both *H. glacialis* and *L. minutus* are found within the metalimnion and therefore follow the dynamics portrayed in Figure 2.8, where animals are patchy at low wind speeds and homogeneous at high winds speeds. Even though *D. thomasi* is found in the hypolimnion, this species demonstrates the same pattern as mentioned above with the metalimnetic species. A possible reason why *D. thomasi* does not share the same negative relationship with its fellow hypolimnetic species could be that this particular copepod is able to swim faster than the other species (Visser et al. 2009). According to Link (1996), even the largest cladoceran, *D. mendotae* was captured 80% of the time in a study of fish-zooplankton contact rates. The smallest cyclopoid was only captured 65%

of the time (Link 1996). Therefore, it is reasonable to suggest that the cyclopoid *D. thomasi* is capable of holding its position in the hypolimnion during low wind speeds compared to its hypolimnetic conspecifics.

Wind direction on the sample day was the only parameter that improved predictions of abundance of *D. mendotae* and *L. minutus*. The explanation for this result is unclear. Why were these the only 2 species that had abundance significantly predicted by wind direction? Why only on the sample day? Further sampling with the consideration of the wind effect on depth would help address these questions.

The inclusion of wind in MLR models helps predict zooplankton abundance beyond year/day of year and chemistry. On average, the inclusion of wind in the 9 MLR models significantly adds 2.4% to the prediction of abundance beyond year/day of year and chemistry, with a total of 22% for all 9 models combined. On larger lakes, the wind effect may be even bigger or smaller. When wind is a considerable factor in a study that may bias results, such as for large lakes, e.g. Lake Ontario, the effect of the wind on species distributions may well be predictable. . If wind can have a predictable effect on zooplankton abundance, we can correct for its influence.

Given the comparisons between year/day of year and chemistry and wind, the order of importance of factors that are needed to predict daily abundance can be hypothesized using the 9 MLR models. Year and day of year have the greatest effect on the change in abundance (of the 9 MLR models, average contribution = 6.6%), while chemistry appears to be less important than year/day of year (4.3%). Wind may matter less when predicting abundance compared to year/day of year and chemistry, but its level

of importance still remains (2.4%). The use of Harp Lake as a study site for documenting the distribution of zooplankton is beneficial because the chemistry has not changed largely over the last 25 years. However, the invasion of *Bythotrephes* may have inflated the effect of year on the abundance of zooplankton species within Harp Lake. Without the *Bythotrephes* invasion, wind might have been more important in the MLR models as year/day of year masked wind as a predictor of abundance.

Sampling zooplankton once at a single station is adequate for capturing a yearly effect because the regression models in this study document a great deal of variation in abundance attributable to year. However day of year and wind may suffer from infrequent samples because seasonality and the wind field change throughout the calendar year. Examining patterns using few sampling days at a single station may not capture the fluctuations in the life history of animals (seasonal) or as the climate warms (decadal). On the other hand, wind can fluctuate daily, even hourly and with few sampling dates, the wind can have a varying effect on zooplankton depending on the strata in which, they are located and the strength of the wind itself. Water chemistry is less of a concern regarding the sampling efficiency in Harp Lake, since the changes observed are more similar over time and less drastic compared to lakes with major water chemistry issues (drastically changing chemistry concentrations). Zooplankton are not used in large bioassessment projects, therefore this study has provided insight to further explore wind as a contributor within aquatic ecosystems as well as demonstrating that zooplankton do in fact react to many predictors.

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Table 2.1: The number of sampling dates available for the chosen species between 1980 and 2004 in Harp Lake, Ontario out of a total of 291 sampling dates.

Species	Total Number of Sample Dates With Abundance Recorded	Percentage of Data Available
D. mendotae	247	85
H. glacialis	200	69
B. tubicen	138	47
D. birgei	132	45
L. sicilis	171	59
L. minutus	268	92
D. thomasi	278	96
T. extensus	263	90

Table 2.2: Summary table of the zooplankton species chosen in Harp Lake between 1980-2004 using the data after substituting the blank values with the lowest detection limit (LDL), N=25 years.

Species	**Average Abundance for all years (#/m^3)**	**Abundance Range between 1980-2004 (lowest to highest)**	**Spearman Correlation between Abundance and Year (r, p-value)**	**TREND**
D. mendotae	579.17	11.44 – 3194.00	0.35, p<0.0001	Increasing
H. glacialis	326.81	5.12 – 3736.40	0.01, p=0.8268	Slightly Increasing
B. tubicen	282.13	3.37 – 9116.47	-0.53, p<0.0001	Decreasing
D. birgei	383.88	4.88 – 1145.87	-0.56, p<0.0001	Decreasing
L. sicilis	121.95	21.81 – 617.20	0.19, p=0.0010	Increasing
L. minutus	690.26	21.71 – 6623.63	-0.19, p=0.0014	Decreasing
D. thomasi	220.97	82.61 – 623.67	-0.09, p=0.1297	Slightly Decreasing
T. extensus	430.84	69.00 – 1520.92	-0.16, p=0.0069	Decreasing

Table 2.3: Regression models predicting abundance of zooplankton species between 1980-2004 using multiple steps: year (Yr) and day of year (DOY).

Species	**Model**	**r^2**	**Fstat/p-value**
D. mendotae	LogAbundance = -4.911+0.06748*DOY-0.0001566*DOY^2+0.03223*Yr	0.54	111.15/<0.0001
H. glacialis	LogAbundance = -30.77+0.5781*DOY-0.003663*DOY^2+1.0046x10^{-5}*DOY^3-1.0215x10^{-8}*DOY^4	0.38	43.62/<0.0001
B. tubicen	LogAbundance = 2.647-0.7458*Yr+0.2187*Yr^2-0.02312*Yr^3+0.0009979*Yr^4-1.5169x10^{-5}*Yr^5	0.37	33.67/<0.0001
D. birgei	LogAbundance = 3.033-0.8475*Yr+0.2391*Yr^2-0.02513*Yr^3+0.001081*Yr^4-1.6389x10^{-5}*Yr^5	0.41	39.83/<0.0001
L. sicilis	LogAbundance = 1.57+0.004171*Yr^2-0.0001594*Yr^3	0.09	14.87/<0.0001
L. minutus	LogAbundance = 55.3-1.389*DOY+0.01421*DOY^2-6.9942x10^{-5}*DOY^3 +1.6453x10^{7}*DOY^4-1.4772x10^{-10}*DOY^5	0.37	32.80/<0.0001
D. thomasi	LogAbundance = 2.67-0.002261*DOY	0.09	28.25/<0.0001
T. extensus	LogAbundance = 1.534+0.004308*DOY-0.011*Yr	0.20	36.48/<0.0001

Table 2.4: Spearman correlation coefficients between the residual abundance of zooplankton and the wind field using the residual abundance generated from the year/day of year models*. Significance denoted by a p-value<0.05 with 95% confidence.

Species	Day	Wind Speed[a] (rs)	Wind Speed (p-value)	Day	Wind Direction[b] (r)	Wind Direction (p-value)
D.mendotae	Sample	0.02	0.7856	Sample	0.117	**0.0190***
	24 Hrs	0.02	0.7770	24 Hrs	0.055	0.4220
	48 Hrs	0.03	0.6265	48 Hrs	0.058	0.3810
H.glacialis	Sample	0.03	0.5831	Sample	0.052	0.4590
	24 Hrs	0.06	0.3070	24 Hrs	0.108	**0.0340***
	48 Hrs	0.06	0.3090	48 Hrs	0.094	0.0770
B.tubicen	Sample	-0.02	0.7958	Sample	0.070	0.2390
	24 Hrs	0.08	0.1992	24 Hrs	0.077	0.1840
	48 Hrs	-0.07	0.2065	48 Hrs	0.072	0.2200
D.birgei	Sample	-0.04	0.5365	Sample	0.042	0.6080
	24 Hrs	-0.02	0.7352	24 Hrs	0.148	**0.0020***
	48 Hrs	-0.14	**0.0184***	48 Hrs	0.038	0.6560
L.sicilis	Sample	-0.02	0.6778	Sample	0.074	0.2060
	24 Hrs	0.02	0.7852	24 Hrs	0.106	**0.0380***
	48 Hrs	-0.06	0.3092	48 Hrs	0.082	0.1410
L.minutus	Sample	0.13	**0.0246***	Sample	0.119	**0.0170***
	24 Hrs	0.14	**0.0141***	24 Hrs	0.09	0.0990
	48 Hrs	0.15	**0.0127***	48 Hrs	0.038	0.6550
D.thomasi	Sample	0.01	0.8078	Sample	0.111	**0.0290***
	24 Hrs	0.06	0.3297	24 Hrs	0.027	0.8070
	48 Hrs	0.01	0.8845	48 Hrs	0.049	0.4950
T.extensus	Sample	0.07	0.2090	Sample	0.040	0.6370
	24 Hrs	0.09	0.1322	24 Hrs	0.054	0.4340
	48 Hrs	0.08	0.1498	48 Hrs	0.074	0.2060

[a]Pearson correlation coefficients using Analyse-it add-on for Excel
[b]Bivariate linear-circular association coefficients using Oriana 4.0

Table 2.5: PCA summary from the 17 chemistry variables from Harp Lake, Ontario and the summary proportions of the greatest variance.

Principal Components	**Eigenvalues**	**% variance explained by the component**	**Chemistry Variable**	**Value**
PC1	6.65	39.17	Cl	0.3281
			Na	0.3589
			SO_4	-0.3502
PC2	3.59	21.16	Gran_Alk	0.3869
			Mg	0.4263
PC3	1.46	8.59	DIC	-0.6733
			TKN	0.4210
PC4	1.03	6.07	DOC	0.6350
			TKN	0.4230
PC5	0.70	4.14	DOC	-0.4847
			TKN	-0.5371
SUM		**79.14**		

Table 2.6: Summary of all possible regression models between zooplankton abundance and predictor(s) in Harp Lake during 1980-2004. Bolded values are the highest r^2 value between the models for each species. The detailed model compositions are found in Tables 2.3, 2.7-2.9, 2.11-2.12, respectively.

Species	**Year/Day of Year**		**Chemistry**		**Wind Field**		**Year/Day of Year & Chemistry***		**Year/Day of Year & Wind Field***		**Chemistry & Wind Field***		**Year/Day of Year & Chemistry & Wind Field***	
	r^2	*p-value*	*r^2*	*p-value*	*r^2*	*p-value*	*r^2*	*p-value*	*r^2*	*p-value*	*r^2*	*p-value*	*r^2*	*p-value*
D. mendotae	**0.54**	**<0.0001**	0.12	<0.0001	0.04	0.0035	0.14	<0.0001	**0.54**	**<0.0001**	0.14	<0.0001	0.17	<0.0001
H. glacialis	**0.38**	**<0.0001**	0.07	<0.0001	0.05	0.0079	0.12	<0.0001	0.07	0.0002	0.10	<0.0001	0.19	<0.0001
B. tubicen	0.37	<0.0001	0.37	<0.0001	0.05	0.0008	**0.39**	**<0.0001**	0.09	<0.0001	0.17	<0.0001	---	---
D. birgei	0.49	<0.0001	0.39	<0.0001	---	----	**0.60**	**<0.0001**	0.27	<0.0001	0.40	<0.0001	0.44	<0.0001
L. sicilis	0.09	<0.0001	0.09	<0.0001	0.02	0.0458	**0.11**	**<0.0001**	---	---	0.06	0.0007	---	---
L. minutus	**0.37**	**<0.0001**	0.04	0.0014	0.08	<0.0001	0.31	<0.0001	0.10	<0.0001	0.09	<0.0001	0.11	<0.0001
D. thomasi	0.09	<0.0001	0.05	0.0013	0.01	0.0469	**0.15**	**<0.0001**	---	---	0.06	0.0004	---	---
T. extensus	**0.20**	**<0.0001**	0.07	0.0002	---	---	0.19	<0.0001	---	---	---	---	---	---

*Must include each of the variables in order to be considered.

Table 2.7: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using chemistry. Computations were done in AI and the r^2 is based on the entire model. PC-principal component.

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= 2.311 - 0.1873*PC2 - 0.1563*PC3	0.12	19.45/p<0.0001
2	*H. glacialis*	LOGAbund= 1.984 - 0.1424*PC3 - 0.1026*PC4	0.07	10.42/p<0.0001
3	*B. tubicen*	LOGAbund= 1.801 - 0.1727*PC1 + 0.3382*PC2 - 0.1734*PC3	0.37	55.11/p<0.0001
4	*D. birgei*	LOGAbund= 1.864 - 0.2281*PC1 + 0.3893*PC2 - 0.179*PC3 - 0.1103*PC4	0.39	45.59/p<0.0001
5	*L. sicilis*	LOGAbund= 1.822 + 0.05134*PC1 - 0.07999*PC2 - 0.06627*PC4 + 0.06866*PC5	0.09	7.05/p<0.0001
6	*L. minutus*	LOGAbund= 2.419 + 0.1113*PC2 - 0.08596*PC4	0.04	6.75/p=0.0014
7	*D. thomasi*	LOGAbund= 2.187 - 0.06788*PC3 - 0.05696*PC4	0.05	6.83/p=0.0013
8	*T. extensus*	LOGAbund= 2.31 - 0.09239*PC1 + 0.09292*PC2 + 0.06623*PC4	0.07	6.96/p=0.0002

Table 2.8: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using wind. Computations were done in AI and the r^2 is based on the entire model. Spd-wind speed, Dir-wind direction, S-sample day, 24-24 hours prior to the sample day, 48-48 hours prior to the sample day, and Spd24xDir24-an interaction term between the 2 predictors

Model #	**Species**	**Model**	**r^2**	**Fstat/p-value**
1	*D. mendotae*	LOGAbund= 2.06 + 0.003223*Dir24 - 0.0005582*Spd24xDir24	0.04	5.77/p=0.0035
2	*H. glacialis*	LOGAbund= 1.011 + 0.1758*Spd24 + 0.004333*Dir24 + 0.002011*Dir48 - 0.0009114*Spd24xDir24 - 0.0003226*Spd48xDir48	0.05	3.20/p=0.0079
3	*B. tubicen*	LOGAbund= 1.435 + 0.1816*Spd24 - 0.0003309*Spd24xDir24	0.05	7.31/p=0.0008
4	*D. birgei*	No model could be produced	---	---
5	*L. sicilis*	LOGAbund= 1.697 + 0.00156*DirS - 0.0002718*SpdSxDirS	0.02	3.12/p=0.0458
6	*L. minutus*	LOGAbund= 1.86 + 0.07736*SpdS + 0.09806*Spd48	0.08	12.06/p<0.0001
7	*D. thomasi*	LOGAbund= 2.072 + 0.03548*Spd24	0.01	3.98/p=0.0469
8	*T. extensus*	No model could be produced	---	---

Table 2.9: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using year/day of year and chemistry. Computations were done in AI and the r^2 is based on the entire model. Yr-year, DOY-day of year, PC-principal component, DOYxYr-an interaction term between the 2 predictors.

Model #	**Species**	**Model**	**r^2**	**Fstat/p-value**
1	*D. mendotae*	LOGAbund= 1.906+0.03092*Yr-0.1232*PC3	0.14	24.12/p<0.0001
2	*H. glacialis*	LOGAbund= 2.666-0.003192*DOY-0.09933*PC1-0.1654*PC3	0.12	12.81/p<0.0001
3	*B. tubicen*	LOGAbund= 0.9111+0.008117*DOY-0.01972*Yr-5.0148x10^{-8}*DOYxYr-0.1275*PC1+ 0.2149*PC2-0.1733*PC3	0.39	30.86/p<0.0001
4	*D. birgei*	LOGAbund= -1.769+0.03066*DOY-0.0377*Yr-2.0749x10^{-7}*DOYxYr-0.1399*PC1+ 0.1657*PC2-0.1292*PC4	0.60	70.82/p<0.0001
5	*L. sicilis*	LOGAbund= 1.57+0.001178*DOY+0.0634*PC1-0.08953*PC2-0.09121*PC4+0.06728*PC5	0.11	6.78/p<0.0001
6	*L. minutus*	LOGAbund= 6.419-0.02635*DOY-0.02216*Yr+1.6422x10^{-7}*DOYxYr-0.09522*PC3	0.31	31.85/p<0.0001
7	*D. thomasi*	LOGAbund= 2.837-0.002546*DOY-0.008081*Yr-0.09486*PC3	0.15	16.77/p<0.0001
8	*T. extensus*	LOGAbund= 1.416+0.004375*DOY-0.04074*$PC3^2$	0.19	34.62/p<0.0001

Table 2.10: Spearman correlation coefficients between the residual abundance of zooplankton and the wind field using the residual abundance generated from the year/day of year and chemistry models. *Significance denoted by a bolded p-value<0.05 with 95% confidence.

Species	Day	Wind Speed[a] (rs)	Wind Speed (p-value)	Day	Wind Direction[b] (r)	Wind Direction (p-value)
D.mendotae	Sample	-0.05	0.3766	Sample	0.11	**0.030***
	24 Hrs	-0.02	0.7542	24 Hrs	0.113	**0.025***
	48 Hrs	-0.12	**0.0338***	48 Hrs	0.1	0.056
H.glacialis	Sample	0.02	0.7658	Sample	0.064	0.310
	24 Hrs	0.04	0.5010	24 Hrs	0.13	**0.007***
	48 Hrs	-0.03	0.5561	48 Hrs	0.038	0.666
B.tubicen	Sample	0.07	0.2555	Sample	0.043	0.589
	24 Hrs	0.11	0.0685	24 Hrs	0.06	0.358
	48 Hrs	0.04	0.4621	48 Hrs	0.081	0.149
D.birgei	Sample	0.06	0.3463	Sample	0.063	0.319
	24 Hrs	-0.03	0.6544	24 Hrs	0.116	**0.021***
	48 Hrs	0.07	0.2241	48 Hrs	0.102	0.051
L.sicilis	Sample	-0.02	0.6909	Sample	0.062	0.326
	24 Hrs	0.03	0.6352	24 Hrs	0.08	0.159
	48 Hrs	-0.05	0.4423	48 Hrs	0.089	0.100
L.minutus	Sample	0.06	0.3216	Sample	0.103	**0.047***
	24 Hrs	0.06	0.2775	24 Hrs	0.117	**0.019***
	48 Hrs	0.08	0.1519	48 Hrs	0.029	0.783
D.thomasi	Sample	0	0.9440	Sample	0.102	**0.049***
	24 Hrs	0.04	0.5306	24 Hrs	0.029	0.785
	48 Hrs	-0.03	0.6340	48 Hrs	0.064	0.303
T.extensus	Sample	0.12	**0.0370***	Sample	0.056	0.410
	24 Hrs	0.13	**0.0245***	24 Hrs	0.069	0.253
	48 Hrs	0.14	**0.0212***	48 Hrs	0.098	0.064

[a]Pearson correlation cefficients using Analyse-it add-on for Excel
[b]Bivariate linear-circular association coefficients using Oriana 4.0

Table 2.11: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using year/day of year and wind. Computations were done in AI and the r^2 is based on the entire model. Yr-year, DOY-day of year, DOYxYr-an interaction term between the 2 predictors. Spd-wind speed, Dir-wind direction, S-sample day, 24-24 hours prior to the sample day, 48-48 hours prior to the sample day, and Spd24xDir24-an interaction term between the 2 predictors

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= -3.237 + 0.03546*DOY + 0.03486*Yr - 2.4122E-007*DOYxYr + 0.08675*Spd48 + 0.001246*DirS - 0.0002767*Spd48xDir48	0.54	56.24/p<0.0001
2	*H. glacialis*	LOGAbund= 1.753 - 0.002374*DOY + 0.1611*Spd24 + 0.004597*Dir24 - 0.001007*Spd24xDir24	0.07	5.75/p=0.0002
3	*B. tubicen*	LOGAbund= 0.7884 + 0.002977*DOY + 0.1155*Spd24	0.09	14.11/p<0.0001
4	*D. birgei*	LOGAbund= -2.859 + 0.03215*DOY - 2.1328×10^{-7}*DOYxYr + 0.1108*SpdS	0.27	36.20/p<0.0001
5	*L. sicilis*	No model could be produced	---	---
6	*L. minutus*	LOGAbund= 2.311 - 0.001887*DOY + 0.06754*SpdS + 0.09267*Spd48	0.10	10.76/p<0.0001
7	*D. thomasi*	No model could be produced	---	---
8	*T. extensus*	No model could be produced	---	---

Table 2.12: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using chemistry and wind. Computations were done in AI and the r^2 is based on the entire model. PC-principal component, Spd-wind speed, Dir-wind direction, S-sample day, 24-24 hours prior to the sample day, 48-48 hours prior to the sample day, and Spd24xDir24-an interaction term between the 2 predictors

Model #	**Species**	**Model**	**r^2**	**Fstat/p-value**
1	*D. mendotae*	LOGAbund= 2.556 - 0.1648*PC2 - 0.1528*PC3 - 0.07561*Spd48	0.14	15.56/p<0.0001
2	*H. glacialis*	LOGAbund= 1.223 - 0.1388*PC3 - 0.09718*PC4 + 0.1697*Spd24 + 0.004238*Dir24 - 0.000912*Spd24xDir24	0.10	6.39/p<0.0001
3	*B. tubicen*	LOGAbund= 1.459 - 0.1696*PC1 - 0.187*PC3 + 0.1046*Spd24	0.17	19.34/p<0.0001
4	*D. birgei*	LOGAbund= 1.645 - 0.2366*PC1 + 0.4097*PC2 - 0.1718*PC3 - 0.106*PC4 + 0.002421*Dir48 - 0.0003716*Spd48xDir48	0.40	32.12/p<0.0001
5	*L. sicilis*	LOGAbund= 1.711 - 0.06733*PC4 + 0.0656*PC5 + 0.001468*DirS - 0.0002666*SpdSxDirS	0.06	4.95/p=0.0007
6	*L. minutus*	LOGAbund= 1.868 - 0.08215*PC4 + 0.07219*SpdS + 0.1004*Spd48	0.09	9.75/p<0.0001
7	*D. thomasi*	LOGAbund= 2.058 - 0.07305*PC3 + 0.0397*Spd24	0.06	6.35/p<0.0001
8	*T. extensus*	No model could be produced	---	---

Table 2.13: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using year/day of year, chemistry and/or wind. Computations were done in AI and the r^2 is based on the entire model. Yr-year, DOY-day of year, PC-principal component, Spd-wind speed, Dir-wind direction, S-sample day, 24-24 hours prior to the sample day, 48-48 hours prior to the sample day, and Spd24xDir24-an interaction term between the 2 predictors. *These models are not included in Table 2.6 because they do not include all predictors (year/day of year, chemistry and wind).

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= 1.905 + 0.02893*Yr-0.1261*PC3-0.06867*Spd48+0.001295*DirS	0.17	15.03/p<0.0001
2	*H. glacialis*	LOGAbund= 1.604-8.6698x10^{-11}*DOY^4+0.153*Spd24+0.003793*Dir24-0.0008904* Spd24*Dir24-0.1537*PC3	0.19	13.01/p<0.0001
3	*D.birgei*	LOGAbund= 2.842-0.06529*Yr-0.1292*PC1-0.246*PC3-0.1066*PC4-0.009998*$Spd48^2$	0.44	45.64/p<0.0001
4	*L.minutus*	LOGAbund= 2.723-0.002419*DOY+0.1141*PC2+0.06788*SpdS	0.09	9.82/p<0.0001
5	*L.minutus*	LOGAbund= 2.65-0.002402*DOY+0.01047*PC2+0.08737*Spd48	0.11	11.52/p<0.0001
6	*L.minutus**	LOGAbund= 2.218+0.09001*PC2+0.0617*Spd24	0.04	6.49/p<0.0001
7	*L.minutus**	LOGAbund= 2.148+0.1056*PC2+0.00141*DirS	0.05	7.49/p<0.0001
8	*L.sicilis**	LOGAbund= 1.886-0.0693*PC4-0.005608*$SpdS^2$	0.04	5.28/p<0.0001
9	*D.thomasi**	LOGAbund= 2.058-0.07305*PC3+0.0397*Spd24	0.06	6.35/p<0.0001

Table 2.14a: A summary of the MLR model breakdown for each predictor based on each of the 9 models in Table 2.13. Blank values indicate that SigmaStat did not compute.

Model	**Species**	**Predictors**	**VIF**	**Individual r^2**	**Individual Tstat/p-value***	**Model Fstat/p-value**	**Model r^2**
1	*D. mendotae*	Yr	1.113	0.11	5.57/<0.0001	15.03/<0.0001	0.18
		PC 3	1.024	0.03	-3.159/0.0020		
		Spd48	**1.083**	**0.02**	**-2.23/0.0270**		
		DirS	**1.023**	**0.02**	**2.33/0.0210**		
2	*H. glacialis*	DOY^4	---	0.11	-5.90/<0.0001	13.01/<0.0001	0.19
		PC 3	1.029	0.06	-4.22/<0.0001		
		Spd24	**7.169**	**0.00**	**-0.06/0.9542**		
		Dir24	**7.168**	**0.00**	**1.48/0.1387**		
		Spd24xDir24	**18.38**	**0.02**	**-2.61/0.0096**		
3	*D. birgei*	Yr	1.158	0.29	-10.67/<0.0001	45.64/<0.0001	0.44
		PC 1	1.053	0.02	-3.50/0.0005		
		PC 3	1.025	0.10	-6.81/<0.0001		
		PC 4	1.001	0.01	-3.02/0.0027		
		$Spd48^2$	**1.079**	**0.02**	**-2.51/0.0127**		
4	*L. minutus*	DOY	1.053	0.04	-3.34/0.0009	9.82/<0.0001	0.09
		PC 2	1.072	0.02	2.95/0.0035		
		SpdS	**1.069**	**0.03**	**2.95/0.0034**		

*These values were generated as the variable was included in the model.

Table 2.14b: A summary of the MLR model breakdown for each predictor based on each of the 9 models in Table 2.13.

Model	**Species**	**Predictors**	**VIF**	**Individual r^2**	**Individual Tstat/p-value***	**Model Fstat/p-value**	**Model r^2**
5	*L. minutus*	PC 2	1.068	0.01	2.27/0.0237	6.49/0.0017	0.04
		Spd24	**1.068**	**0.03**	**2.78/0.0058**		
6	*L. minutus*	DOY	1.041	0.04	-3.34/0.0009	11.52/<0.0001	0.11
		PC 2	1.081	0.03	2.72/0.0070		
		Spd48	**1.068**	**0.04**	**3.86/0.0001**		
7	*L. minutus*	PC 2	1.003	0.03	2.76/0.0061	7.49/0.0007	0.05
		DirS	**1.003**	**0.02**	**2.68/0.0077**		
8	*L. sicilis*	PC 4	1.003	0.03	-2.66/0.0083	5.28/0.0056	0.04
		$SpdS^2$	**1.003**	**0.01**	**-1.85/0.0653**		
9	*D. thomasi*	PC 3	1.009	0.03	-3.04/0.0026	6.35/0.0004	0.06
		PC 4	1.000	0.02	-2.35/0.0195		
		Spd24	**1.009**	**0.01**	**2.00/0.0469**		

*These values were generated as the variable was included in the model.

Table 2.15: Summary table of the chemistry variables in Harp Lake, Ontario from 1980 – 2004. N=25 years.

Chemistry Variables	**Annual Average**	**Data Range from 1980-2004 (lowest to highest)**	**Spearman Correlation between Data values and Year (rs, p-value)**	**TREND**
Gran_Alk (mg/L)	3.48	2.84 – 3.98	0.44, p<0.0001	Increasing
Ca (mg/L)	2.85	2.65 – 3.06	-0.55, p<0.0001	Decreasing
Cl (mg/L)	1.94	0.79 – 3.14	0.87, p<0.0001	Increasing
Cond (μS/cm)	35.86	32.76 – 38.72	0.51, p<0.0001	Decreasing
DIC (mg/L)	1.51	1.20 – 1.98	0.08, p=0.2382	Slightly Increasing
DOC (mg/L)	3.80	3.47 – 4.10	0.23, p=0.0006	Increasing
Fe (μg/L)	63.57	35.91 – 124.70	-0.74, p<0.0001	Decreasing
K (mg/L)	0.52	0.46 – 0.57	-0.49, p<0.0001	Decreasing
Mg (mg/L)	0.88	0.80 – 1.02	-0.37, p<0.0001	Decreasing
Na (mg/L)	1.62	0.84 – 2.25	0.93, p<0.0001	Increasing
NH_4/NH_3 (μg/L)	10.23	0.50 – 25.38	0.61, p<0.0001	Increasing
NO_3/NO_2 (μg/L)	105.61	78.31 – 150.00	0.39, p<0.0001	Increasing
TKN (μg/L)	218.31	166.32 – 260.67	0.15, p=0.0246	Increasing
pH	6.29	6.12 – 6.61	0.65, p<0.0001	Increasing
TP (μg/L)	6.58	4.90 – 9.50	-0.60, p<0.0001	Decreasing
SiO_3 (mg/L)	1.45	0.93 – 1.91	0.65, p<0.0001	Increasing
SO_4 (mg/L)	7.01	5.86 – 8.45	-0.86, p<0.0001	Decreasing

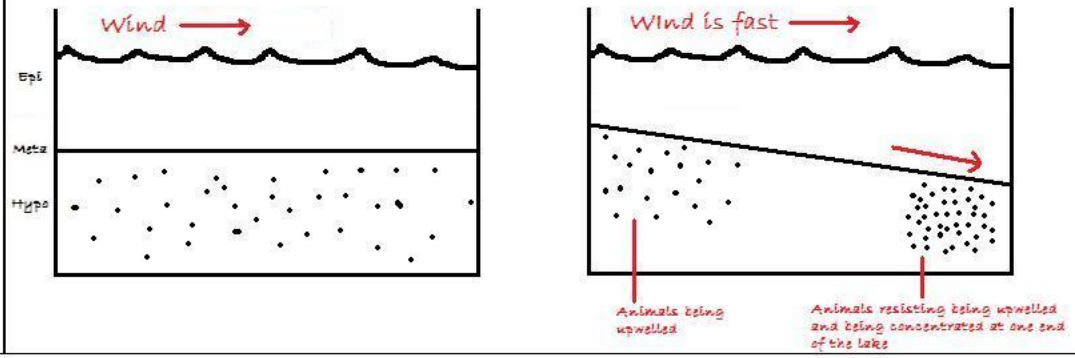
Wind Condition	Wind Behaviour	Wind & Animal Result
Low Wind Speeds		- Animals are more abundant at lower wind speeds. - Animals can hold their position in the water and withstand the currents
High Wind Speeds		- Animals are less abundant at higher wind speeds. - Animals are either resisting being upwelled and are being concentrated at one end of the lake OR the animals are being upwelled.

Figure 2.1: Hypothetical wind dynamics in Harp Lake – A negative relationship between abundance and the predictor wind speed.

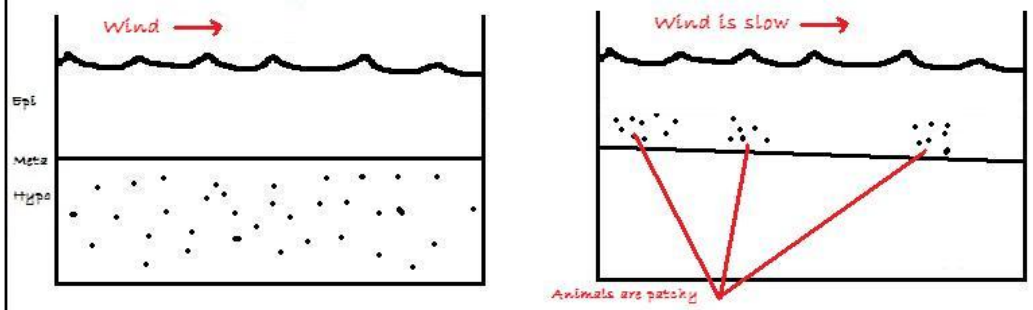
Wind Condition	Wind Behaviour	Wind & Animal Result
Low Wind Speeds		- Animals are less abundant at low wind speeds - Animals are able to withstand the current speeds and become patchy (hold their position in the water)
High Wind Speeds		- Animals are more abundant at high wind speeds - Animals are not able to withstand the current speeds and they are homogeneously distributed in the water column

Figure 2.2: Hypothetical wind dynamics in Harp Lake – A positive relationship between abundance and the predictor wind speed.

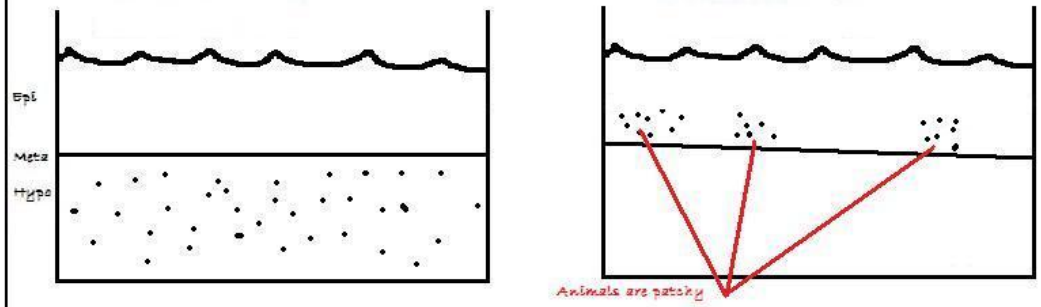
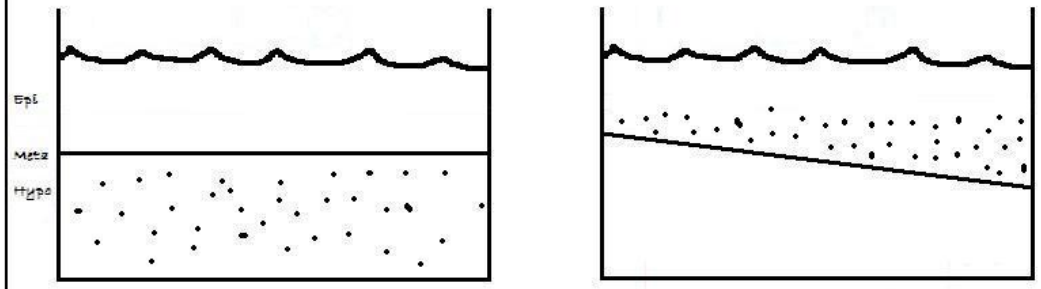
Possibilities	Abundance Dynamics	Animal Result
Case 1 - Fast Animals		*Animals are moving* *Without wind, the currents are still in motion* *Animals that can swim faster than the current would be able to hold their position in the water and become patchy*
Case 2 - Slow Animals		*Animals are being moved* *Without wind, the currents are still in motion* *Animals that cannot swim faster than the current would not be able to hold their position in the water become homogeneously distributed in the water*

Figure 2.3: Hypothetical abundance dynamics in Harp Lake without wind.

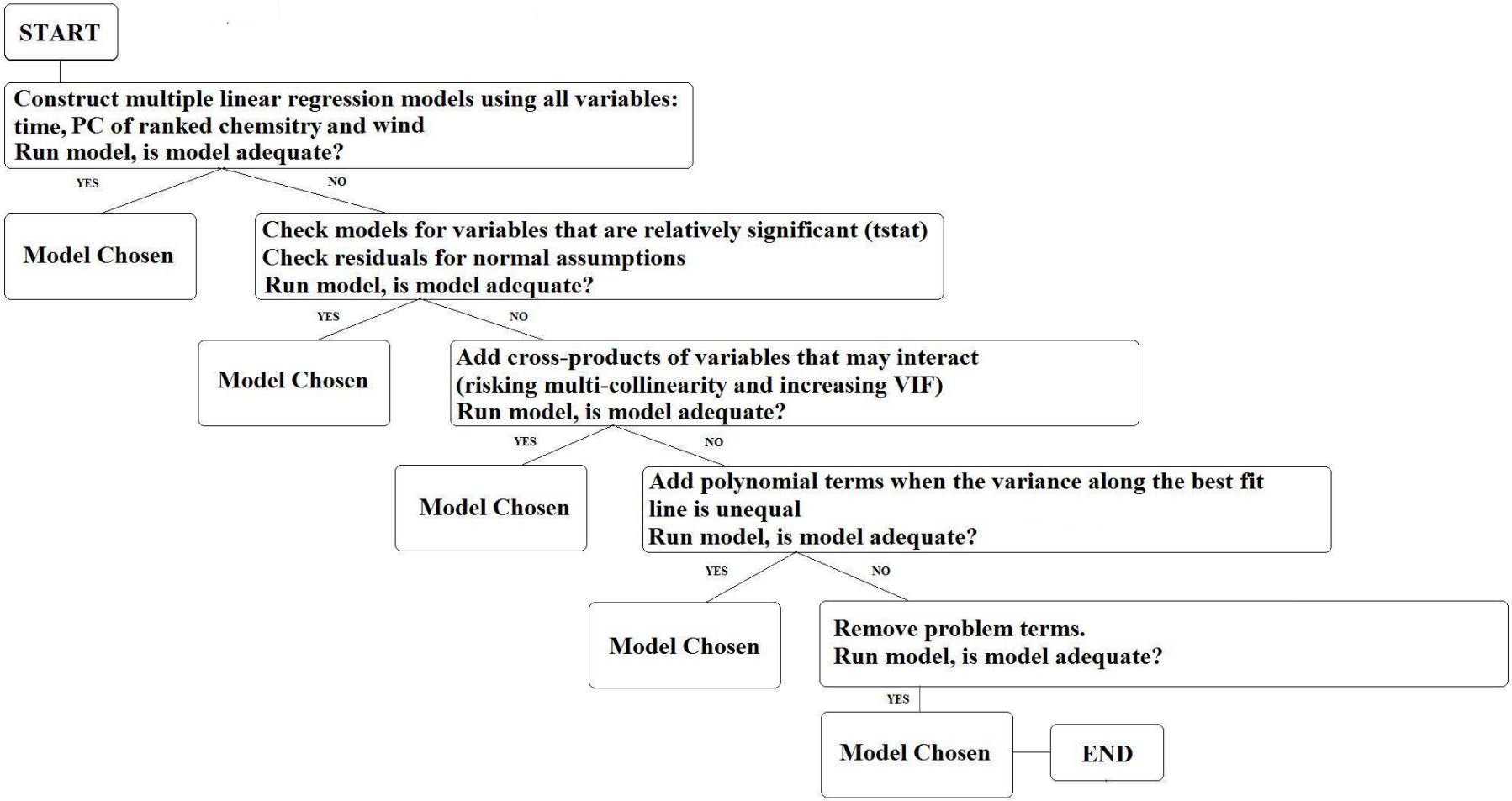


Figure 2.4: Flow chart of the decision making for the multiple regression models in order to better predict zooplankton abundance in Harp Lake, Ontario using year/day of year, chemistry and wind.

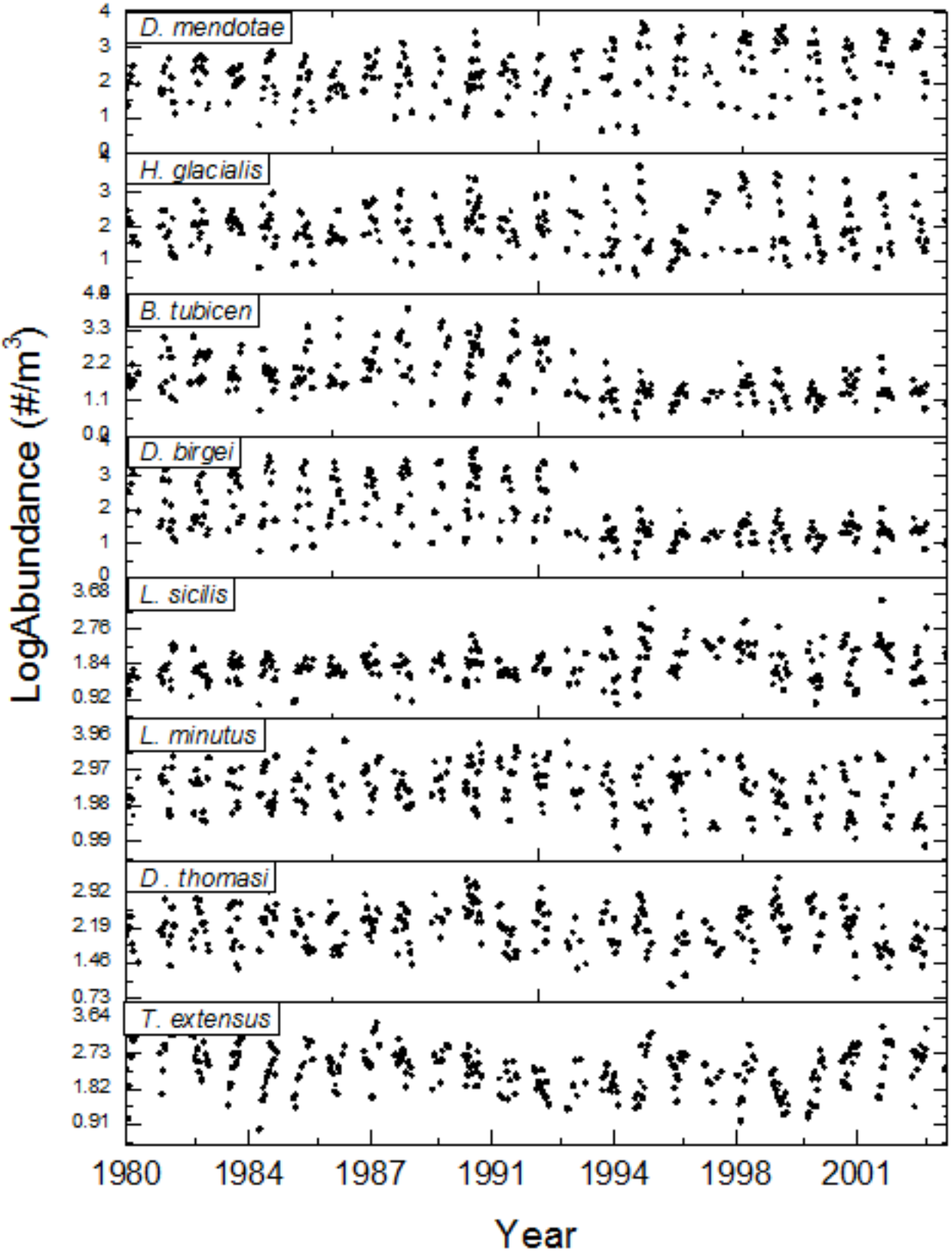


Figure 2.5: Long-term patterns in the chosen zooplankton species in Harp Lake, Ontario between 1980-2004.

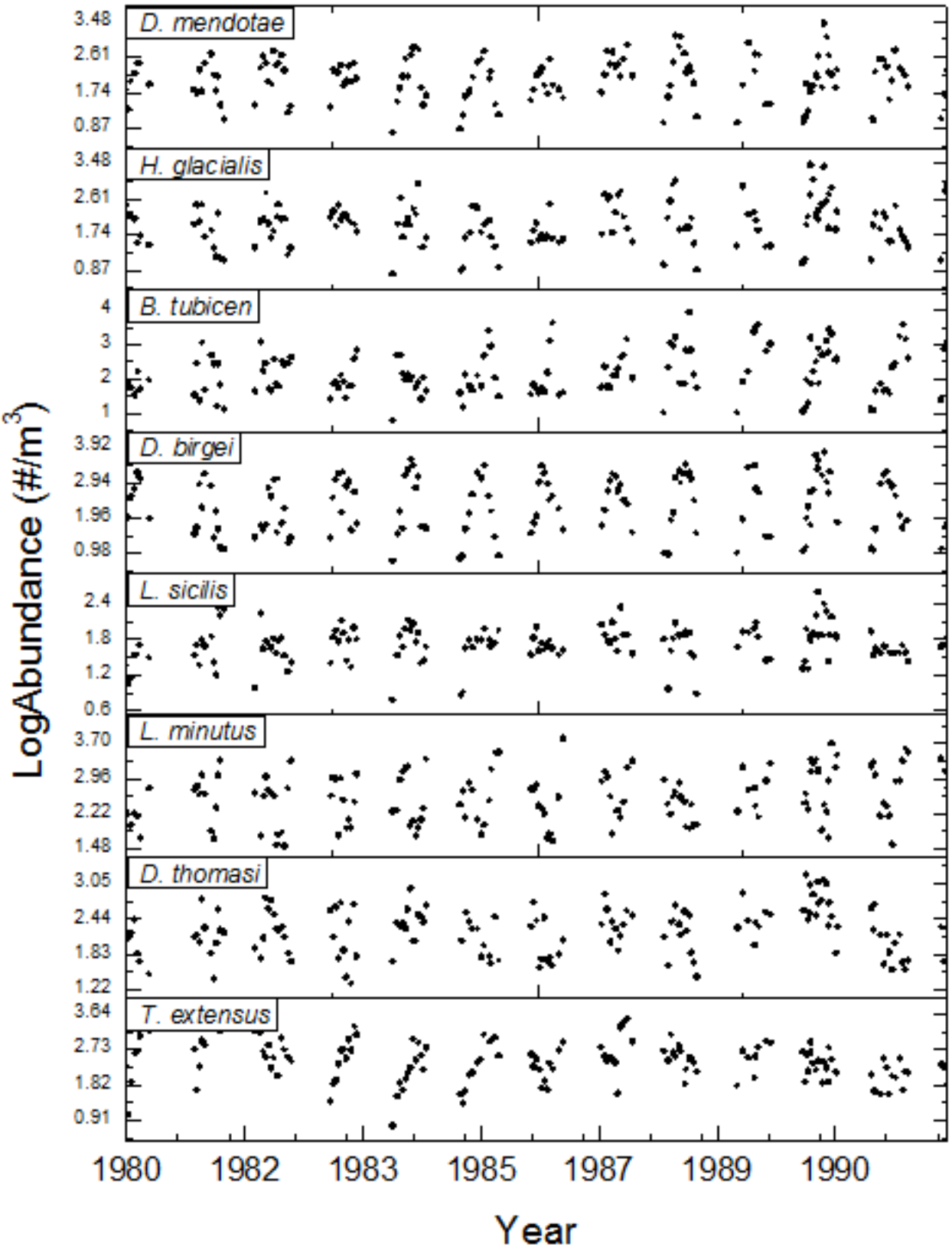


Figure 2.6: Long-term patterns in the chosen zooplankton species in Harp Lake, Ontario between 1980-1992 (pre-*Bythotrephes* presence).

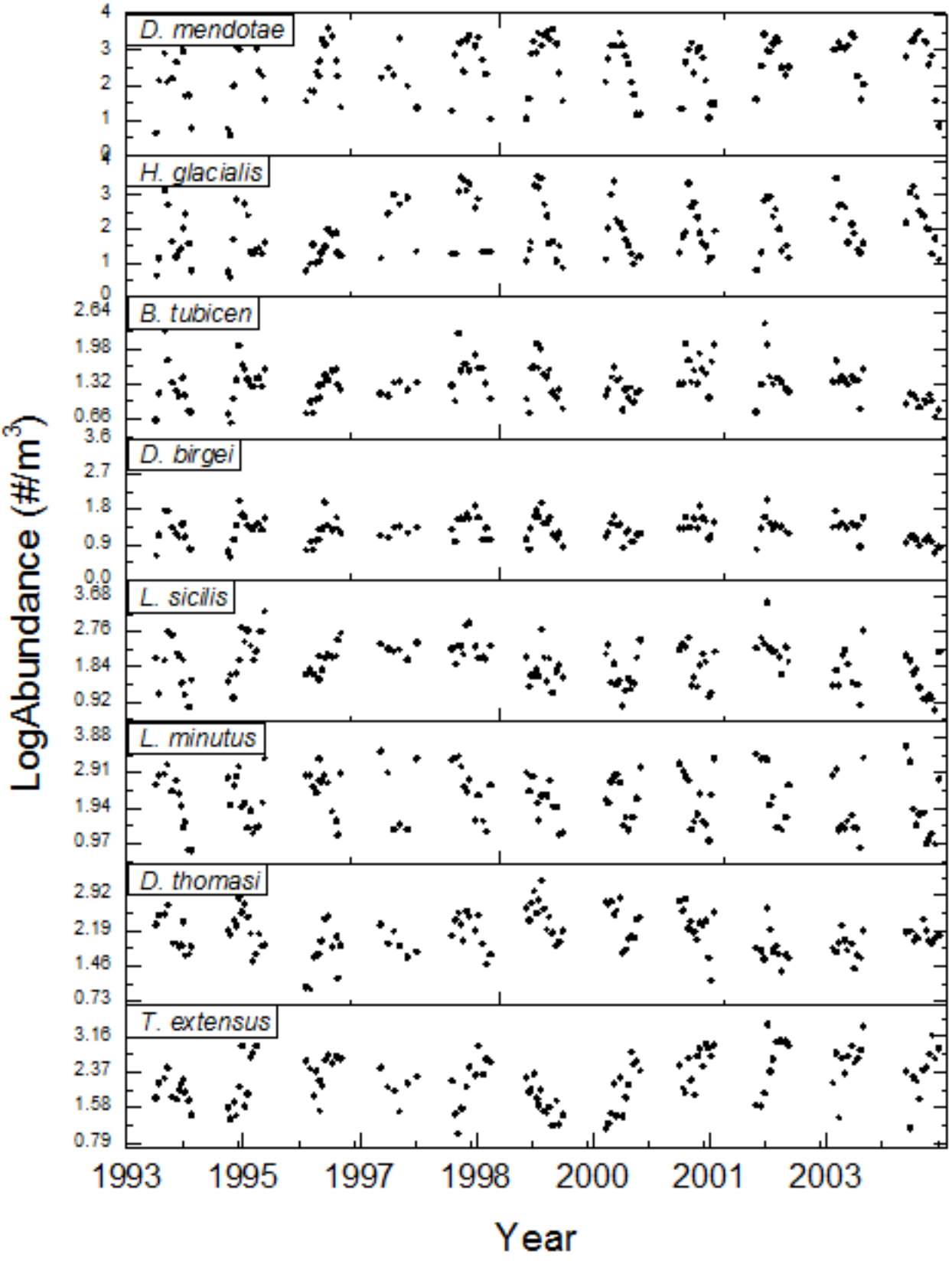


Figure 2.7: Long-term patterns in the chosen zooplankton species in Harp Lake, Ontario between 1993-2004 (post-*Bythotrephes* presence).

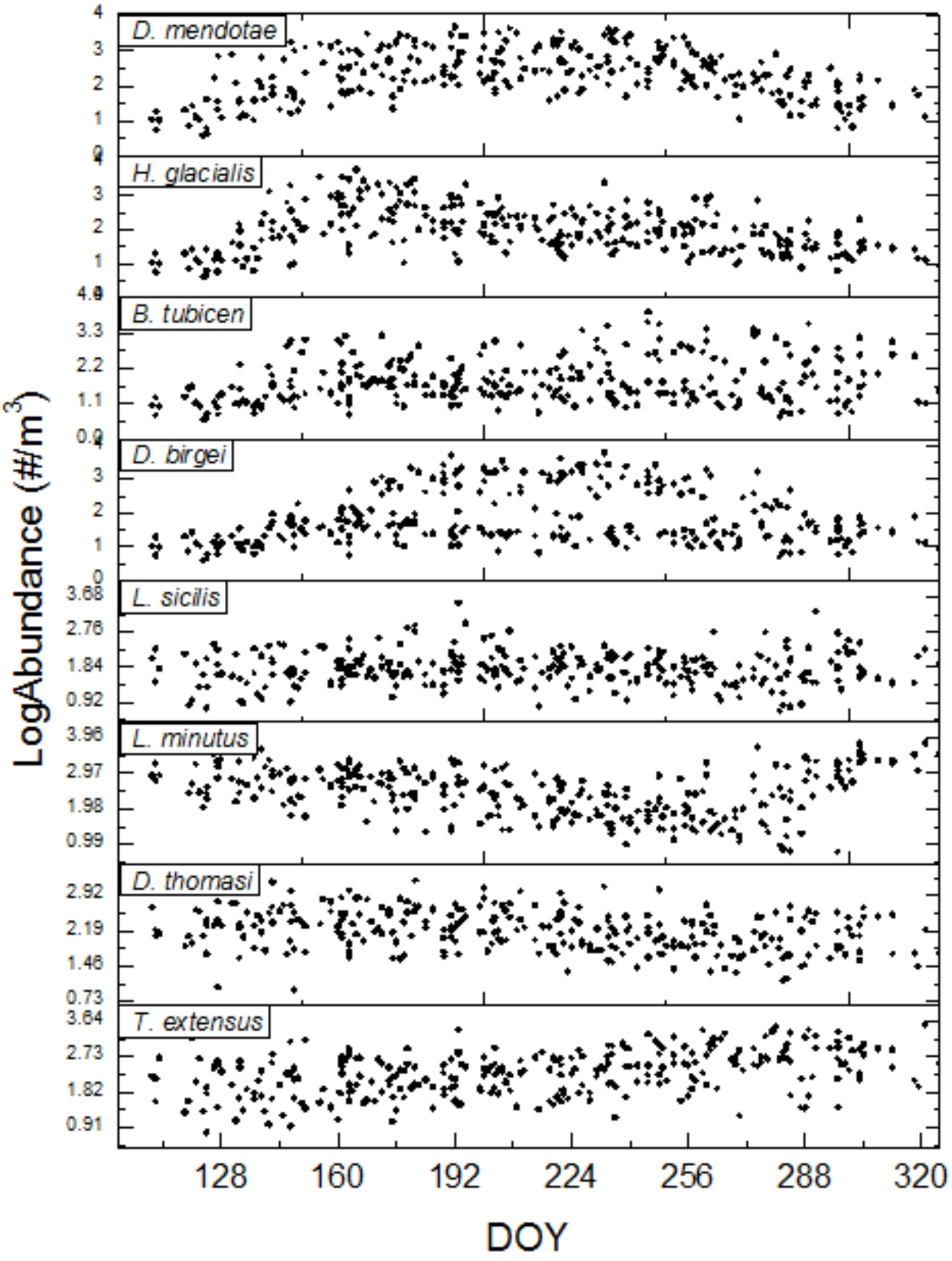


Figure 2.8: Long-term patterns in the chosen zooplankton according to day of year (DOY) in Harp Lake, Ontario between 1980-2004.

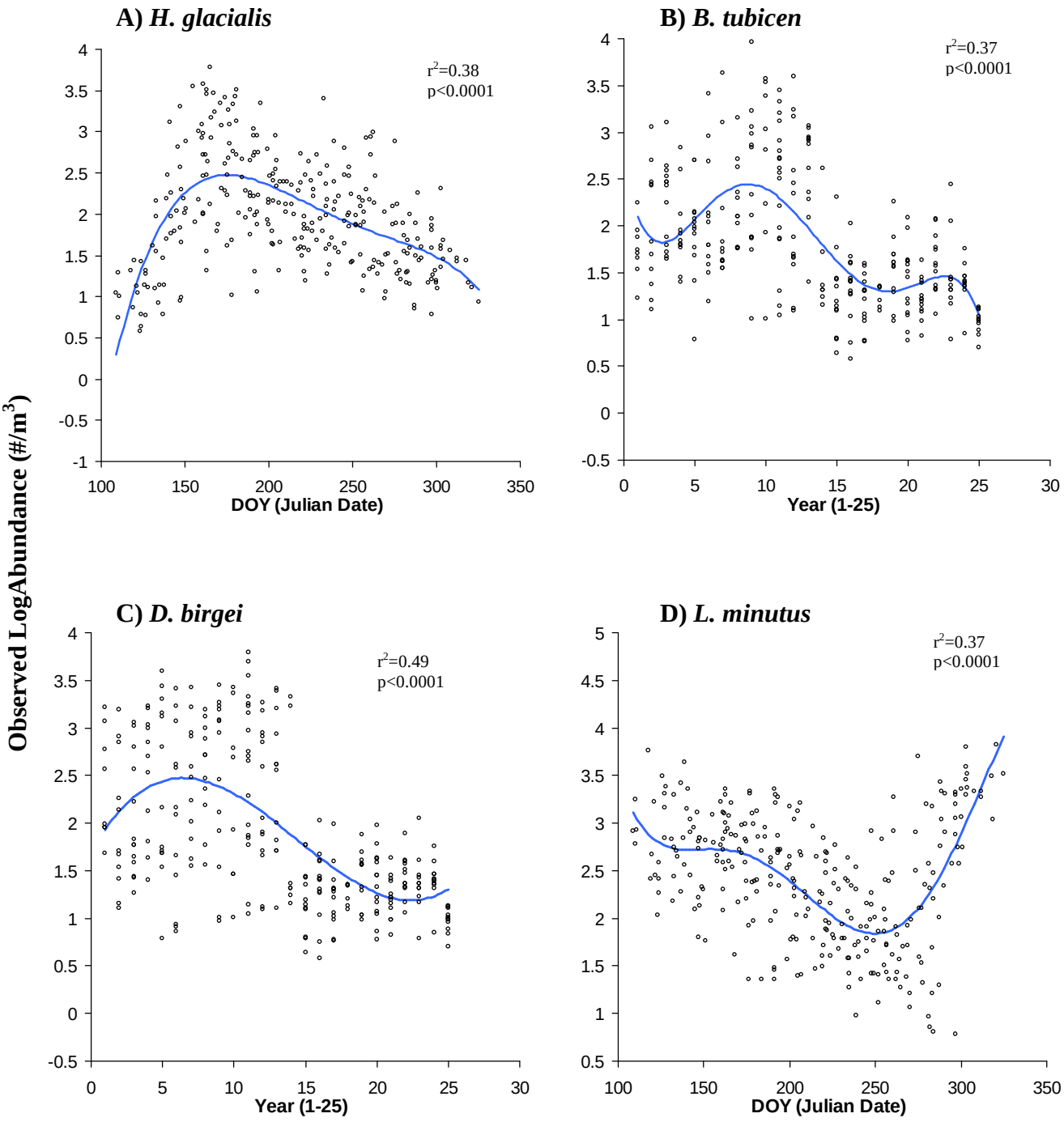


Figure 2.9a: Regression models that best fit the data using the abundance of zooplankton species using multiple steps: year (1-25) and day of year (Julian date).

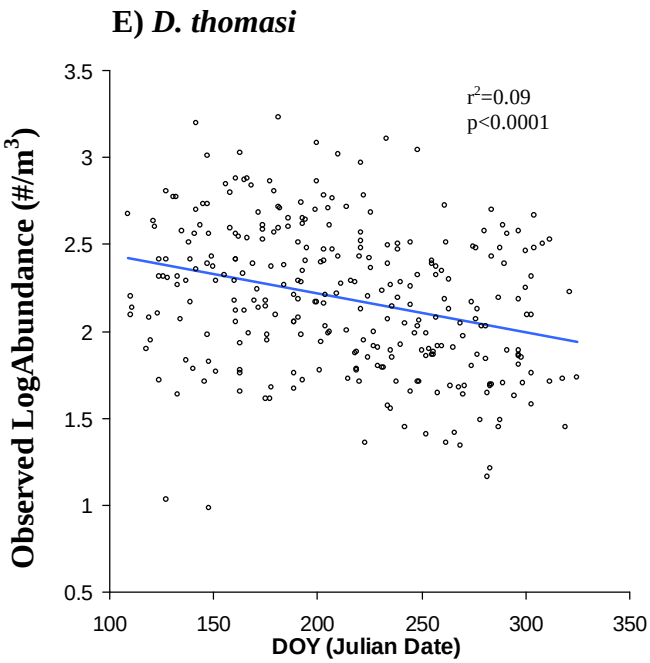


Figure 2.9b: Regression models that best fit the data using the abundance of zooplankton species using multiple steps: year (1-25) and day of year (Julian date).

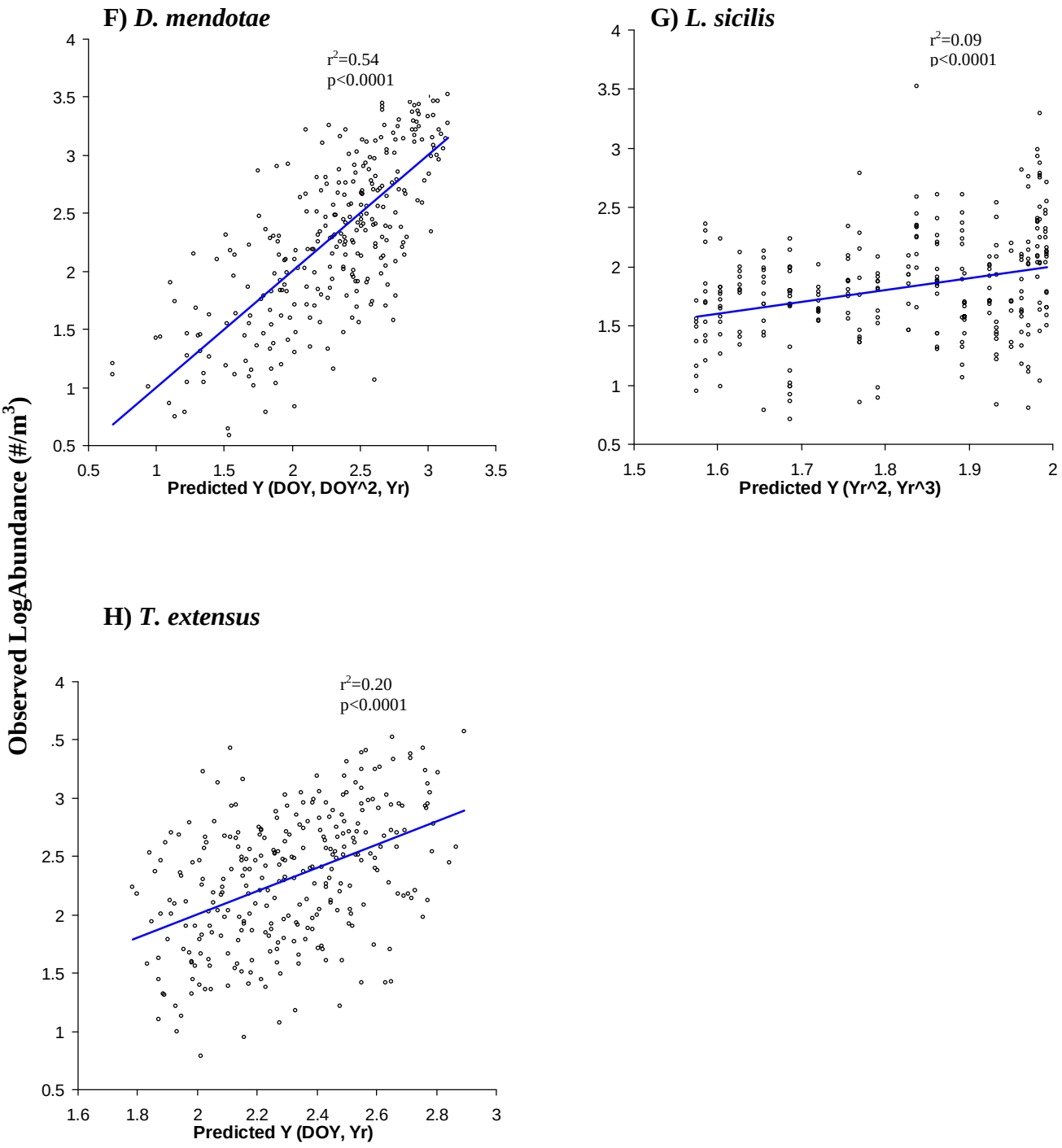


Figure 2.9c: Regression models that best fit the data using the abundance of zooplankton species using multiple steps: year (1-25) and day of year (Julian date).

General Conclusion

The objective of my study was to identify if there is a predictive relationship between zooplankton abundance and the wind field in Harp Lake ON, a lake with a multi-year fortnightly zooplankton data set. This objective was accomplished in 2 steps: 1) by correlating both annual and daily abundance with the wind field after correcting the data for variability attributable to seasonality, warming waters and/or the invasion of *Bythotrephes,* and 2) to determine if the inclusion of the wind field would improve the predictability of abundance in multiple linear regression models, beyond what could be predicted by year/day of year and chemistry. I discovered that the residual abundance in the multiple regression models was correlated with the wind field using daily data (Chapter 2), especially for metalimnetic species but not for annual data (Chapter 1). This result was logical since the wind effect lessens with depth (Bengtsson 1978, Kalff 2002). In Chapter 2, the inclusion of wind with year, Julian day and chemistry revealed that wind better predicts abundance in complex model approaches (regardless of wind being masked by year/day of year and/or chemistry) and that it validates the 'multiple driving forces' hypothesis (the biological-physical-chemical interactions, Pinel-Alloul and Ghadouani 2007).

In particular, in Chapter 1 I began by indicating that both average annual wind speed and direction have changed near Harp Lake, with speed declining by 25%, and winds shifting several degrees to the NW. I determine what fraction of annual variation in abundance of 8 zooplankton species could be attributable first to *Bythotrephes* P/A, average surface temperature on sampling days or average interval between spring ice-

breakup and the days of sampling. I then determined if the residual abundance was correlated with the annual average wind speed and/or direction on the sample dates. These results revealed that wind direction was better correlated with residual abundance with only *D. mendotae* abundance (r^2=0.2333, p=0.005). Thus at annual steps wind speeds in Muskoka were not useful predictors of abundance of most zooplankton in Harp Lake. These results may differ in larger water bodies, in which differing circulation patterns can occur (Deser et al. 1999). Because daily or hourly wind data is commonly used to capture the dynamics in small lakes such as Harp Lake (Waife and Frid 1996, Deser et al. 1999, Antenucci and Imberger 2003), I next examined if wind effects might be discernable within seasons in the lake.

In Chapter 2, I followed a similar approach to chapter 1, but ran the regressions on the daily, not the annually averaged data. In this chapter I also corrected for variance that could be attributed to changes in chemistry, and I considered the wind not just on the day of sampling, but also 1 and 2 days before sampling. The residual abundance was correlated with the wind field for 21% of possible models (wind speed and direction for the abundance of 8 species, on the day of, and 1 and 2 days before sampling). There were 6 significant wind direction, and 4 significant wind speed correlations with abundance. Therefore, the wind direction was slightly more important when predicting residual abundance after considering effects of year and day of year.

Wind speed was a minor driver when predicting abundance in the multiple linear regression models compared to those generated using year/day of year and chemistry (Chapter 2). The prediction of abundance of 6 of the 8 chosen species was improved by

the inclusion of year/day of year, chemistry and wind. Within the models, wind itself contributed between 1-4% of the variation when predicting abundance. Despite the modest contribution, wind did significantly contribute to the model. The ratio of cases where the wind direction and wind speed has a significant contribution to the models was 2:8, respectively. In this case, the wind speed was more important than wind direction when predicting daily zooplankton abundance. Therefore, using the MLR models, the wind direction and speed effect is reversed compared to the correlations between the wind field and residual abundance (after correcting for year/day of year). These results are consistent with the literature that suggests wind speed governs the distribution of organisms in the water; however wind direction was not considered (Owens 1989, MacKenzie and Leggett 1991, Blukacz et al. 2009). For example, Blukacz et al. 2009 found that wind direction did not have a significant relationship between wavelet slopes (indicator of circulation) and that direction was not necessary to consider for the generation of Langmuir circulations. All things considered, the wind field does have a small predictive effect on abundance.

Future work should include carefully synchronized samples with zooplankton abundance and the activity of the wind on a daily basis to better associate the relationship between abundance and the wind field. This approach is confirmed by studies that have investigated various distributions governed by the wind field (George and Edwards 1976, Elci 2008, Blukacz et al. 2009). For example, the 'conveyor belt hypothesis' is described as the motion of wind-driven currents in stratified lakes and that the internal wave period varies dependent on the scale of the basin (Blukacz et al. 2009). At larger scales, the

water circulation can take up to 12 hours to circulate, whereas, at smaller scales the circulation could take up to 20 minutes. Harp Lake is a relatively small lake (71.4 ha) (Yan and Pawson 1997) and Petruinak (2009) found that the internal wave period is 3 hours (~160 minutes) and that sampling should be done daily as oppose to taking yearly averages. Therefore, using hourly abundance and wind data would be more beneficial to documenting the effect of the wind on the movement of the animals in the water.

Further research could involve a better understanding of the hydrodynamics in Harp Lake to help explain why the animals are located in specific areas during a wind event. As in Chapter 1 and 2, the significant correlations/associations of abundance with the wind field were somewhat puzzling because smaller yearly scales and their relative abundance were not used. For instance, in Chapter 2, *D. thomasi* was found to positively correlate with the wind speed 24 hours prior to the sample date in the multiple linear regression models. I speculated that *D. thomasi* were more abundant at higher wind speeds because the wind tilted the thermocline leading to a downwind accumulation of *D. thomasi*. Previously, it was clear that the wind could influence zooplankton abundance on particular days, especially after prolonged unidirectional wind events along the long axis of lakes. Here, I have provided, some, albeit weak evidence that consideration of the wind might improve the prediction of long-term zooplankton abundance patterns, even those determined at single sampling stations. The implications of this research may be far-reaching in the field of aquatic ecology if they can be shown to occur in other lakes. It is well known that the wind induces water currents and causes the movement of any object suspended within the water (George and Edwards 1976, Pinel-Alloul and

Ghadounani 2007). However, not until now has there been a study that proves wind can have a predictive relationship with zooplankton abundance, especially when combined with year/day of year and chemistry over long-time series in Canadian lakes.

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Appendix 1: Treating missing data in the zooplankton abundance dataset

The errors associated with using daily data

How to deal with missing data?

After extracting the daily data from the database and organizing the zooplankton abundances by all sampling dates (n=291), blank values were observed for some of the species at particular sample dates. The number of blanks or missing data per species varied and had to be dealt with in order to analyse the data accurately. The lowest and highest percentages of data available were from D. birgei and D. thomasi, respectively (Table 1.1). Why were the blanks an issue when analysing this dataset? Since the number of blank spaces varied for each of the species, the analyses for those species with more blanks would have results greatly biased based on the sample size. The issue with analysing data with blanks or missing data not only creates issues with sample size but what does a missing value mean? Were the species truly absent on the sample day? Is this blank the absence of the animal? Is this blank due to counting error and the animal was not recognized among the sample? Was the fraction of the sample analyzed too small? Was the animal not counted from the sample because only half of the animal was present? It is hard to discern what a missing value could be.

Table 1.1: Summary table of counting error parameters

Species	**Mean[1]**	**Sample Size**	**Variance**	**Precision Coefficient of Variation (scale of 0 – 1)[2]**
D. mendotae	18.26	247	454.15	0.43
H. glacialis	11.25	200	218.11	0.52
B. tubicen	9.54	138	166.47	0.62
D. birgei	13.26	132	168.93	0.60
L. sicilis	7.25	171	75.69	0.65
L. minutus	21.42	268	800.05	0.41
D. thomasi	8.59	278	79.72	0.48
T. extensus	15.34	263	270.57	0.42

[1]The mean is the average number of individuals counted in the sample of the fraction analysed.
[2]The higher the value, the lower the precision of the sample.

What options are available for correcting missing data?

Since the number of blank dates varied for each of the species, analysing the abundance data would be greatly biased for a particular species that had very little data recorded (such as *D. birgei*). As a default, most researchers will leave the missing data out (Allison 2002). This is known as listwise/casewise deletion (Allison 2002). There are assumptions made when dealing with missing data: the data are missing completely at random (MAR), the data are ignorable or the data are non-ignorable and need a good estimate to be substituted if the value is not MAR (Allison 2002). There are a few options available to correct for the missing data that follow the assumptions mentioned. (1) The blanks may have indicated that the animals were not found or counted in that sample and that the blank was correct, therefore the blanks were left in the dataset and used in the analyses (n=varies/species). This method is called listwise deletion (Allison 2002). (2) The blanks may have indicated that the animals were not present at the sample station when the sample was taken and the value should have been entered as zero, therefore the blank would be replaced by a zero (n=291/species) This method is called imputation with a reasonable substitution for a missing value (Allison 2002). However, the zero may be animals that were present in the sediment as resting eggs or immatures that were not identified to species; therefore the zero value may be a seasonal artefact. A seasonal artefact would be defined as a zero value that indicates an animal was not present but in fact, the animal should have been present because the sample date was during a peak season in the abundance of the species. This would be considered a possible error caused by counting. Seasonal artefacts were not included in the analyses

because only 2 of the 8 species indicated possible seasonal artefacts (*D. mendoate* and *L. minutus*). *L. minutus* abundance demonstrated a seasonal trend (using DOY) that deviated from the expected reproductive cycle (Antonsson 1992) and may have been inaccurate because only adults are included in the data values. Finally, (3) The blanks may have been an artefact of the counting error and animals were actually present, therefore the blank would be replaced by the lowest detection limit in the fraction analysed for that sample date (n=291/species). This method is also called imputation with a reasonable substitution for a missing value (Allison 2002).

In order to calculate the lowest detection limit, the maximum fraction analysed of the sample and the sample volume on a particular sample date were used. This calculation gives the chance of finding 1 individual in the maximum fraction analysed for all species in the count of a particular sample. The numerator is multiplied by 10^3 because the animal abundances extracted from the database are recorded in number of individuals per m^3 ($\#/m^3$). All sample sizes for each zooplankton species will be 291 dates because all missing values are replaced by the LDL. The imputation method where blanks were replaced by a zero in the dataset disregards potential small values and would not give an accurate estimate of the abundance trends in the analyses. The LDL method would give the best estimate of what the blanks may be. In fact, the LDL values are based on standardized sample volumes and an exact fraction analysed of the sample. The values that were extracted from the database are the values that were counted and therefore include the error associated with counting (refer to the NUM_CT mean and variation

below). The LDL method was used to calculate the blanks in the abundance for this study as oppose to the aforementioned methods.

In order to determine the error associated with the actual count of individuals I assumed that the distribution of individuals in the counting cells would follow a Poisson distribution. Therefore, following McCauley (1984), I estimate the theoretical precision of the count from the coefficient of variation of the number of animals counted for each species. The precision coefficient of variation is used to determine the accuracy of the counting error on a scale of 0 to 1. The larger the precision coefficient of variation, the greater the inaccuracy of the count. While, the lower the coefficient, the better the accuracy of the count of the sample. This calculation is defined as

Precision Coefficient of Variation $= \frac{1}{\sqrt{NUM\_CT}}$ (McCauley 1984) Equation 1.1

where NUM_CT is the number of animals counted in a sample for a species.

Assessment of the counting error (NUM_CT)

The error associated with the counting of the zooplankton sample from Harp Lake, Ontario varies by species (Table 1.1). The greatest mean NUM_CT was for *L. minutus*, which was 21.42 animals counted in the fraction of the sample taken. However, *L. minutus* also held the greatest variation amongst the NUM_CT values (800.05). The lowest mean NUM_CT was for *L sicilis,* which was 7.25 animals counted and with a low variance of 75.69. The average precision coefficient of variation between 1980-2004 varied among the species with a range of 0.41 to 0.65 (Figure 1.1). The greater the

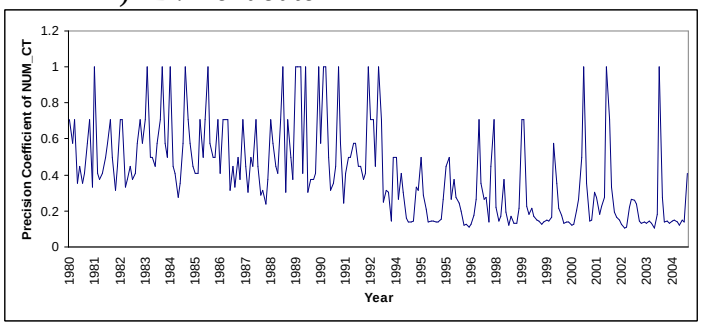
coefficient, the lower the precision of the count of the sample. As an example, *L. minutus* had the lowest average precision of 0.41 or 41%, which is not surprising because of its high mean NUM_CT but seems a little shocking because of the high variance between the NUM_CT's. Refer to Figure 1.2a-b for graphical plots of the annual average precision coefficient of variation values for each species.

Total error associated with each of the nine models.

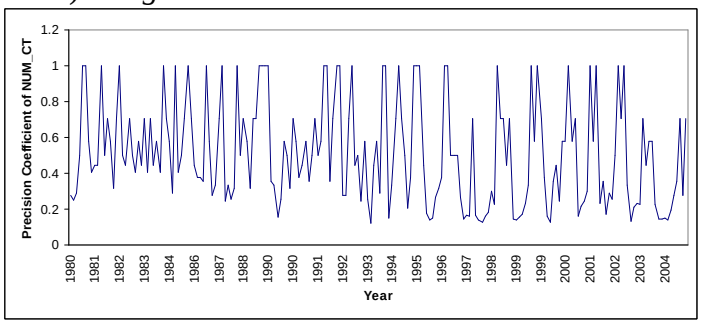
The distribution of error that explains the variation in zooplankton abundance is apparent from the pie charts in Figure 1.2a-b, where the precision coefficient of variation percent is, in most cases the largest source of error. Each of the 9 models has particular proportions defined by the following: Yr, DOY, chemistry, wind, precision coefficient of variation percentage and/or unknown error. For Yr/DOY, chemistry and wind, the values included in the chart are the values obtained from the stepwise multiple regression r^2 values for each predictor (done in SYSTAT SigmaStat). Model 3, or the model that better predicts the abundance of *D. birgei* has a total value of error proportions larger than 100% (Table 1.2). This in itself shows the error in sampling.

Precision coefficient of variation percent for counting error

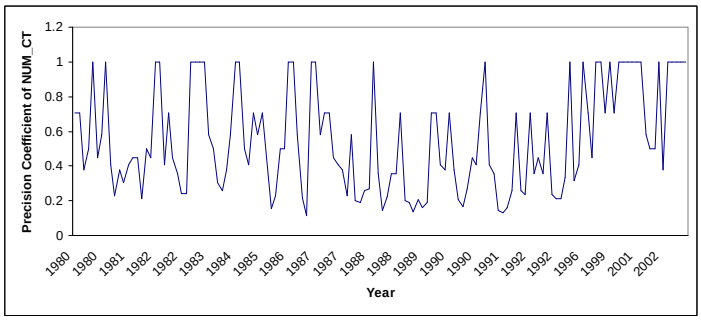
A) *D. mendoate*



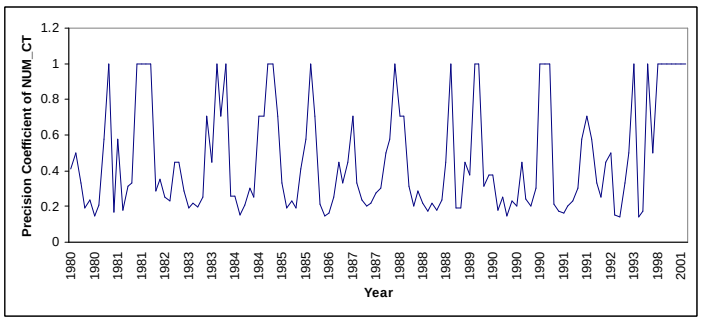
B) *H. glacialis*



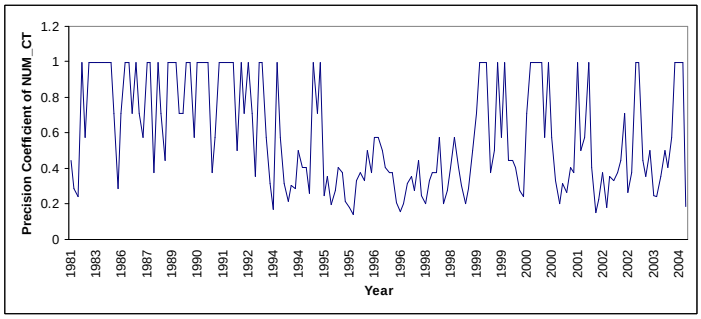
C) *B. tubicen*



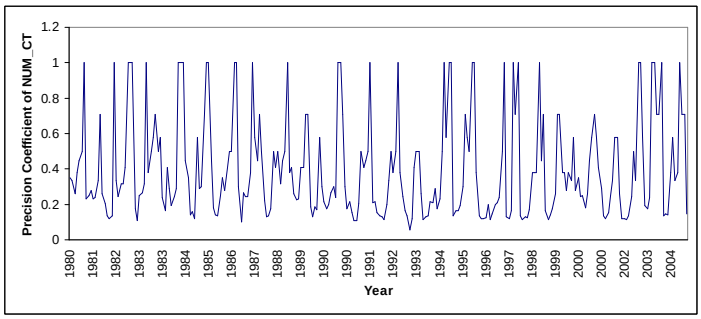
D) *D. birgei*



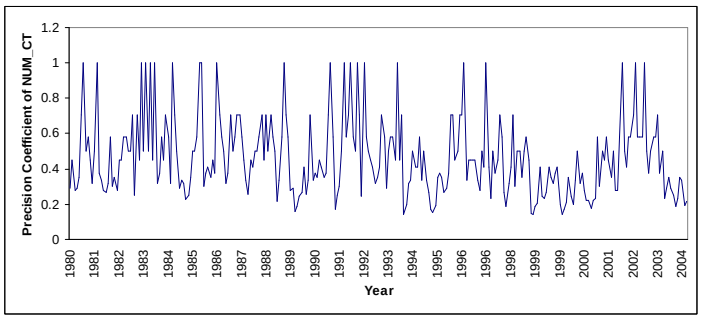
E) *L. sicilis*



F) *L. minutus*



G) *D. thomasi*



H) *T. extensus*

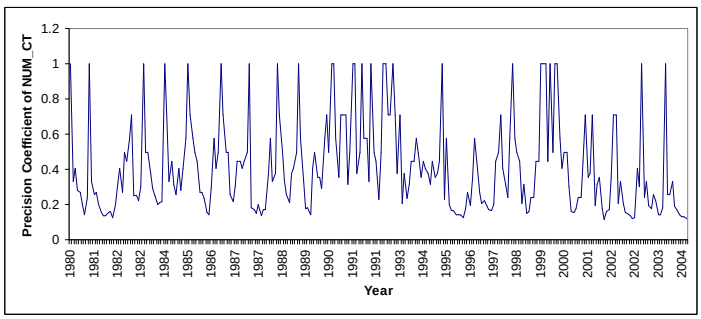
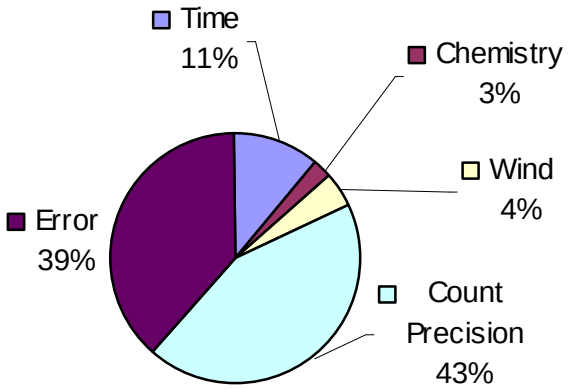
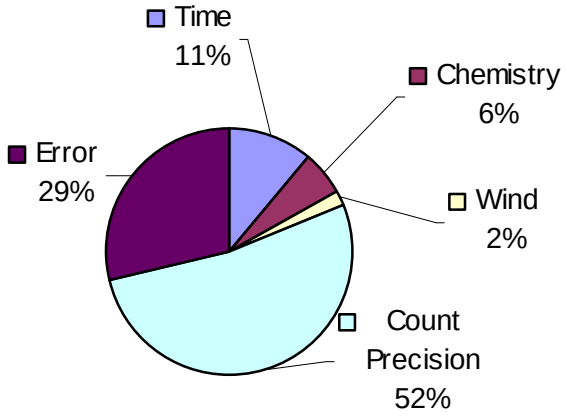


Figure 1.1: Precision coefficient of variation percentage for counting error of number of individuals (NUM_CT).

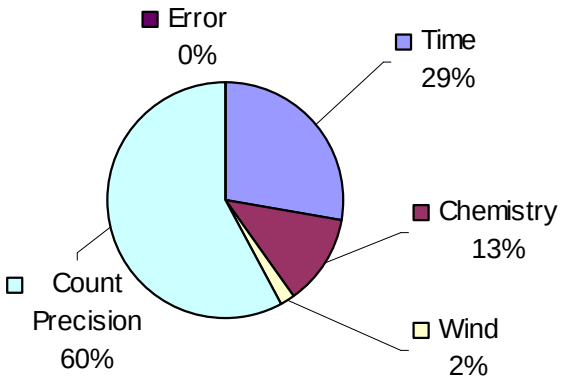
Model 1 – *D. mendotae*



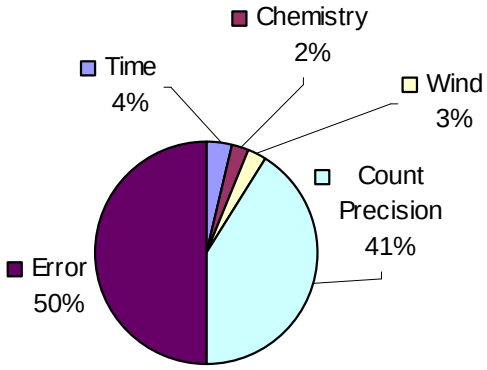
Model 2 – *H. glacialis*



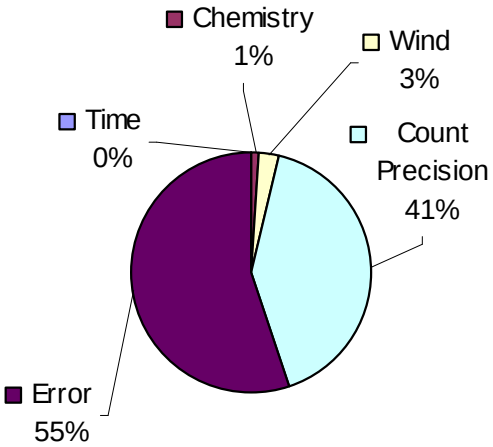
Model 3 – *D. birgei*



Model 4 – *L. minutus*



Model 5 – *L. minutus*



Model 6 – *L. minutus*

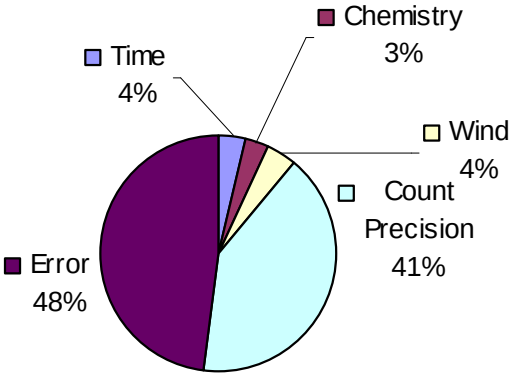
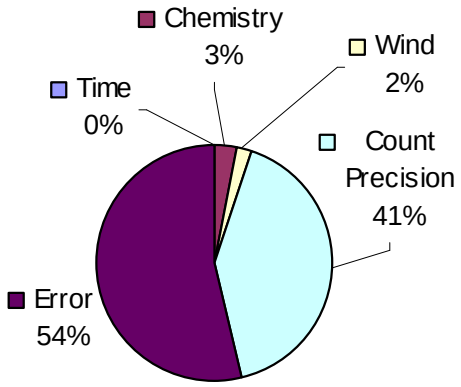
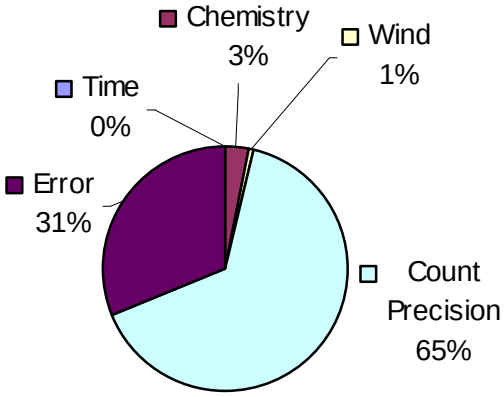


Figure 1.2a: Pie charts depicting each of the models error proportions. The models used are those from Table 2.13.

Model 7 – *L. minutus*



Model 8 – *L. sicilis*



Model 9 – *D. thomasi*

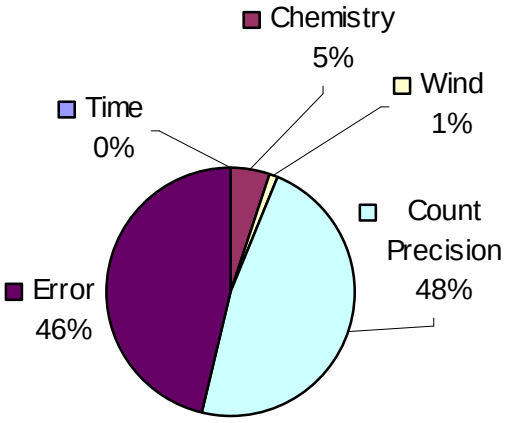


Figure 1.2b: Pie charts depicting each of the models error proportions. The models used are those from Table 2.13.

Table 1.2: Summary of data of the error proportions for each of the twelve regression models generated in Table 1.1.

Models	Yr and DOY	Chemistry (PCs)	Wind Field (speed and direction)	Precision Coefficient of Variation %	Unknown Error
1	11	3	4	43	39
2	11	6	2	52	29
3	29	13	2	60	-4
4	4	2	3	41	50
5	0	1	3	41	55
6	4	3	4	41	48
7	0	3	2	41	54
8	0	3	1	65	31
9	0	5	1	48	46

Appendix 2: How to identify an association between residual abundance and the wind direction using annual averages (Chapter 1).

Wind Direction

Correlations between residual abundance and wind direction are defined by r^2 and the corresponding p-value. The two-sample linear-scatterplot will have the residual abundance that is associated with the wind direction from that particular year. If there is a significant association between residuals and wind direction, the p-value will be less than 0.05 (95% confidence) (Figure 2.1). This indicates that there is not a complementary relationship between the residual abundance data and the wind directions. In other words, the positive and negative residual abundance will not share a similar range in wind directions and will be associated uniquely to a range of directions. Such a case is shown below:

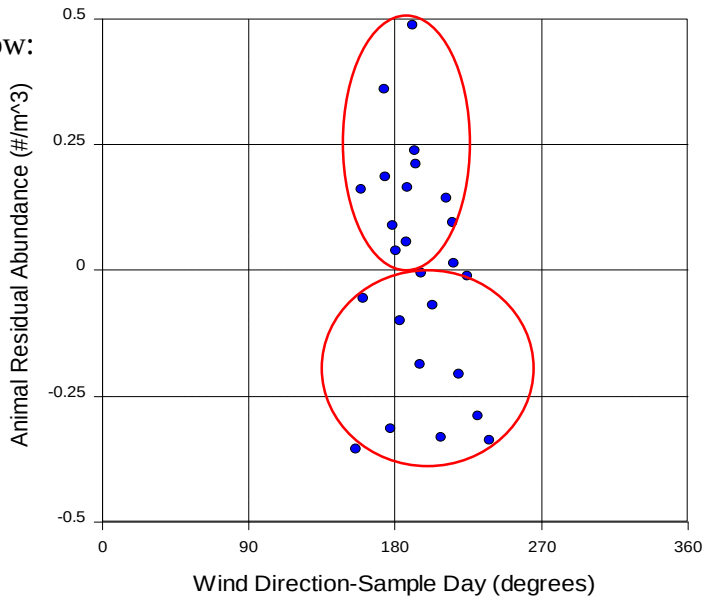


Figure 2.1: Hypothetical representations of the hypothesis that the residual abundance of zooplankton species is uniquely associated with the wind direction over Harp Lake, Ontario. Comparisons were carried out using linear-circular association between the two variables in Oriana 3.0. The circles indicate the various orientations of the data points. Residuals were generated using multiple regressions carried out using Analyse-it add-on for Excel between zooplankton abundance and various metrics: year, degree days and/or days since ice off.

If there is no association between the residuals and wind direction, the p-value will be greater than 0.05 and will have an r^2 value close to 0 (Figure 2.2). This indicates that there is a complementary relationship between the positive and negative residual abundance with similar wind directions. In other words, the positive and negative residual abundances will have a similar relationship to a particular range of wind directions. Such as case is shown below:

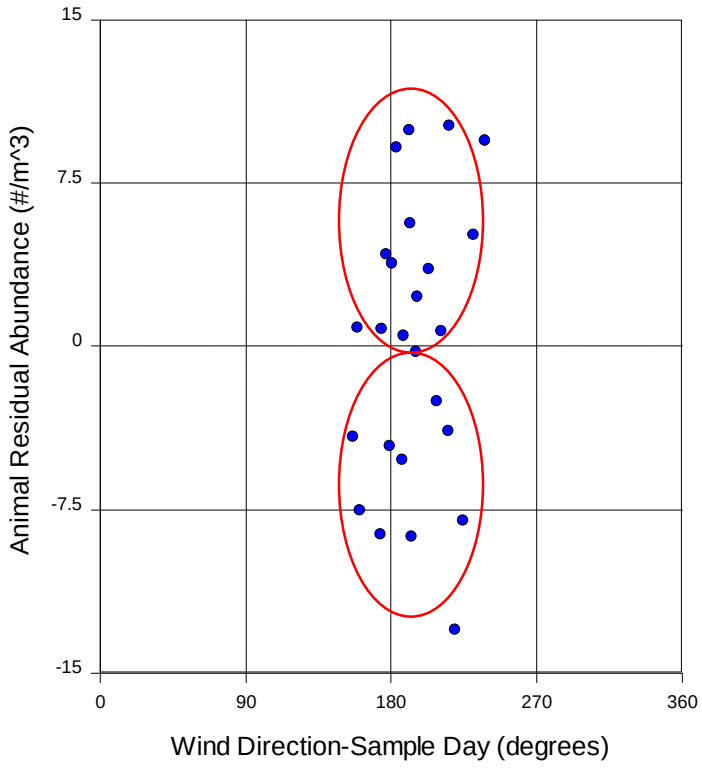


Figure 2.2: Hypothetical representations of the hypothesis that the residual abundance of zooplankton species is not uniquely associated with the wind direction over Harp Lake, Ontario. Comparisons were carried out using linear-circular association between the two variables in Oriana 3.0. The circles indicate the general orientation of the data points. Residuals were generated using multiple regressions carried out using Analyse-it add-on for Excel between zooplankton abundance and various metrics: year, degree days and/or days since ice off.

An association or non-complementary relationship indicates that the swimming orientation of the animal can be predicted by the wind direction, where the animals can be found in a particular type of wind direction during that sampling event.

Appendix 3: How to identify an association between residual abundance and the wind field using daily data (Chapter 2).

The two-sample linear scatterplots generated in Oriana 4.0 can depict correlations between residual abundance and wind direction from Chapter 2 to analyze the different distributions of the positive and negative residuals amongst the wind directions in order to observe significant associations. In other words, are the distributions or spread of the positive and negative residuals complementary to a similar range of wind directions? For example, the plot below depicts a data set containing the residual abundance of *D.mendotae* and the associated wind directions (Figure 3.1). Each dot depicts a particular sample date with a residual abundance value and its associated wind direction on that sample date (in this case, 24 hours prior to the sample date).

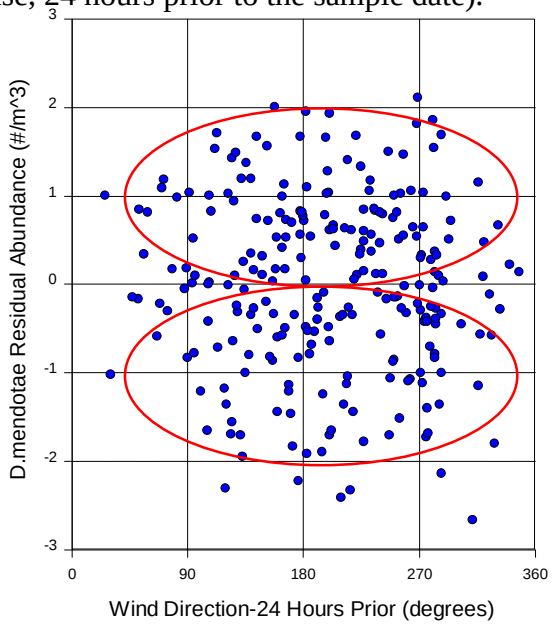


Figure 3.1: Hypothetical representations of the hypothesis that the residual abundance of zooplankton species is not significantly associated with the direction over Harp Lake, Ontario. Comparisons were carried out using bivariate linear-circular associations between the two variables in Oriana 4.0. Residuals were generated using multiple regressions carried out using Analyse-it add-on for Excel between zooplankton abundance and various metrics: year (1-25) and day of year (Julian date). Each circle pertains to either the distribution of the negative or positive residuals.

The circles indicate the balanced complementary relationship between the residuals and the wind direction for both positive and negative residuals (alike to Appendix 1 for Chapter 1). This particular plot indicates that there is no significant association or different relationship between the residuals and wind direction, where the p-value is >0.05 (95% confidence). This indicates that the abundance of animals, either higher or lower than the long-term mean, do not demonstrate any particular long-term trend in wind direction and can potentially orient themselves in the water to a desired direction.

In the case of a significant association between the residuals and the wind direction (or a non-complementary relationship), the following plot would be observed (Figure B4).

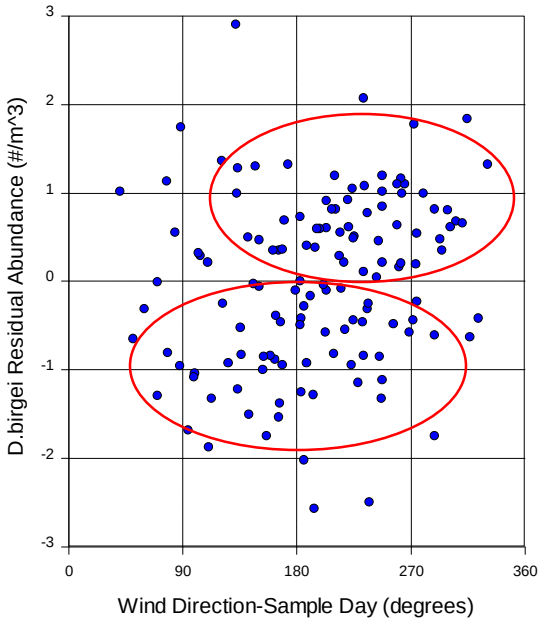


Figure 3.2: Hypothetical representations of the hypothesis that the residual abundance of zooplankton species is significantly associated with the direction over Harp Lake, Ontario. Comparisons were carried out using bivariate linear-circular associations between the two variables in Oriana 4.0. Residuals were generated using multiple regressions carried out using Analyse-it add-on for Excel between zooplankton abundance and various metrics: year (1-25) and day of year (Julian date). Each circle pertains to either the distribution of the negative or positive residuals.

Again, the circles indicate the relationship between the residuals and the wind direction for both positive and negative residuals. However in this case the circles (or distribution of residuals) are not complementary to each other and that the negative residuals associate to a particular range of wind directions, and vice versa with the positive residuals. This plot indicates that there is a significant association or no complementary relationship between the residuals and wind direction, where the p-value is <0.05 (with 95% confidence). In other words, the majority of animals that are found to be more abundant than the long-term mean tend to be directed from the 180-270 degrees range (moving towards N and E). Whereas, the majority of animals that are lower than the long-term mean tend to be directed from the 90-260 degrees range (or moving towards W and NE). This association suggests that the animals may be moving in whichever wind direction that is being observed that day. Therefore, the abundance of animals can be predicted by the particular wind direction observed that day.

Appendix 4: Wind field correlations

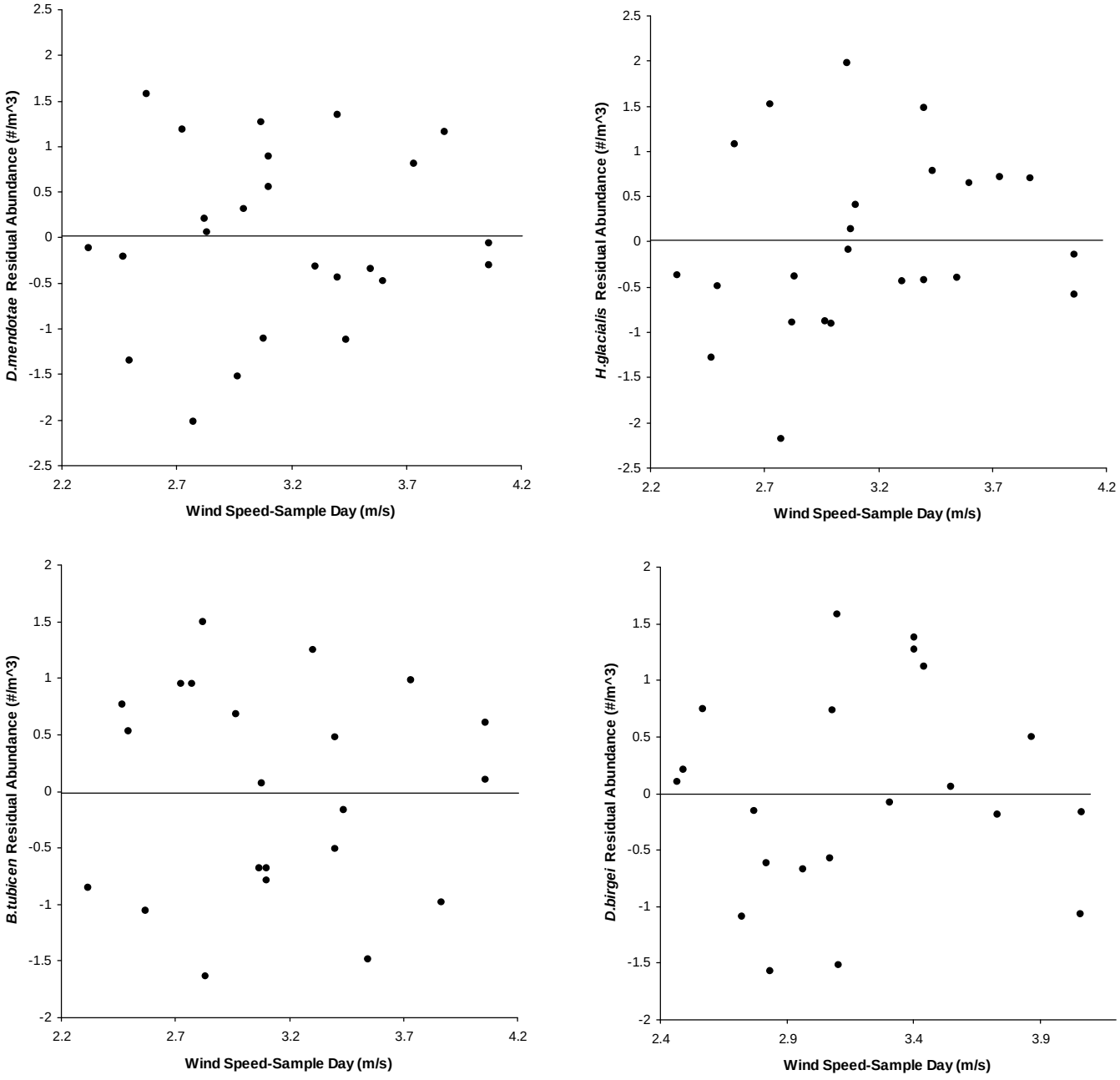


Figure 4.1a: Scatterplots depicting the average annual residual abundance of the chosen zooplankton species and the wind speed over Harp Lake, Ontario during 1980-2004.

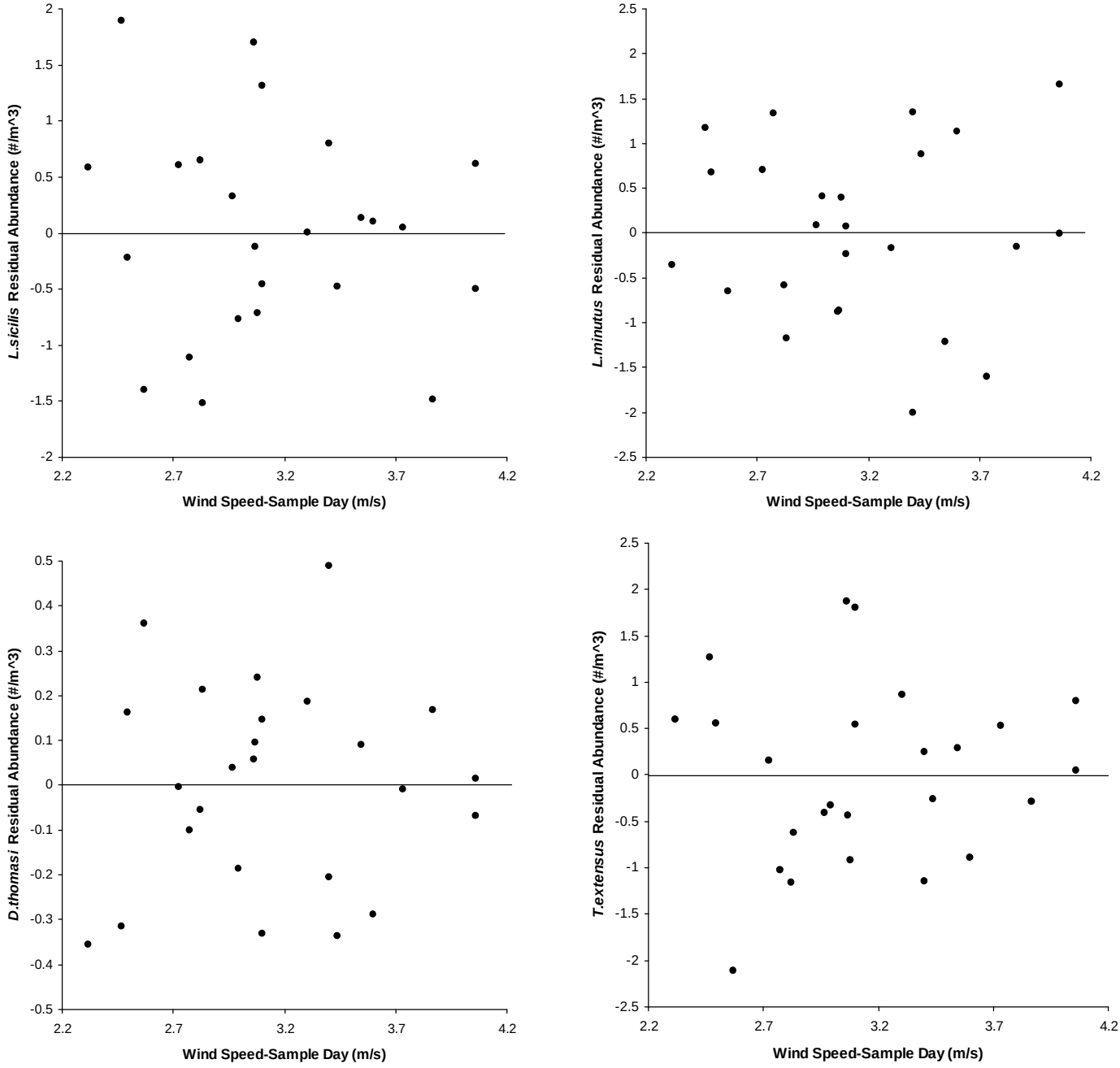


Figure 4.1b: Scatterplots depicting the average annual residual abundance of the chosen zooplankton species and the wind speed over Harp Lake, Ontario during 1980-2004.

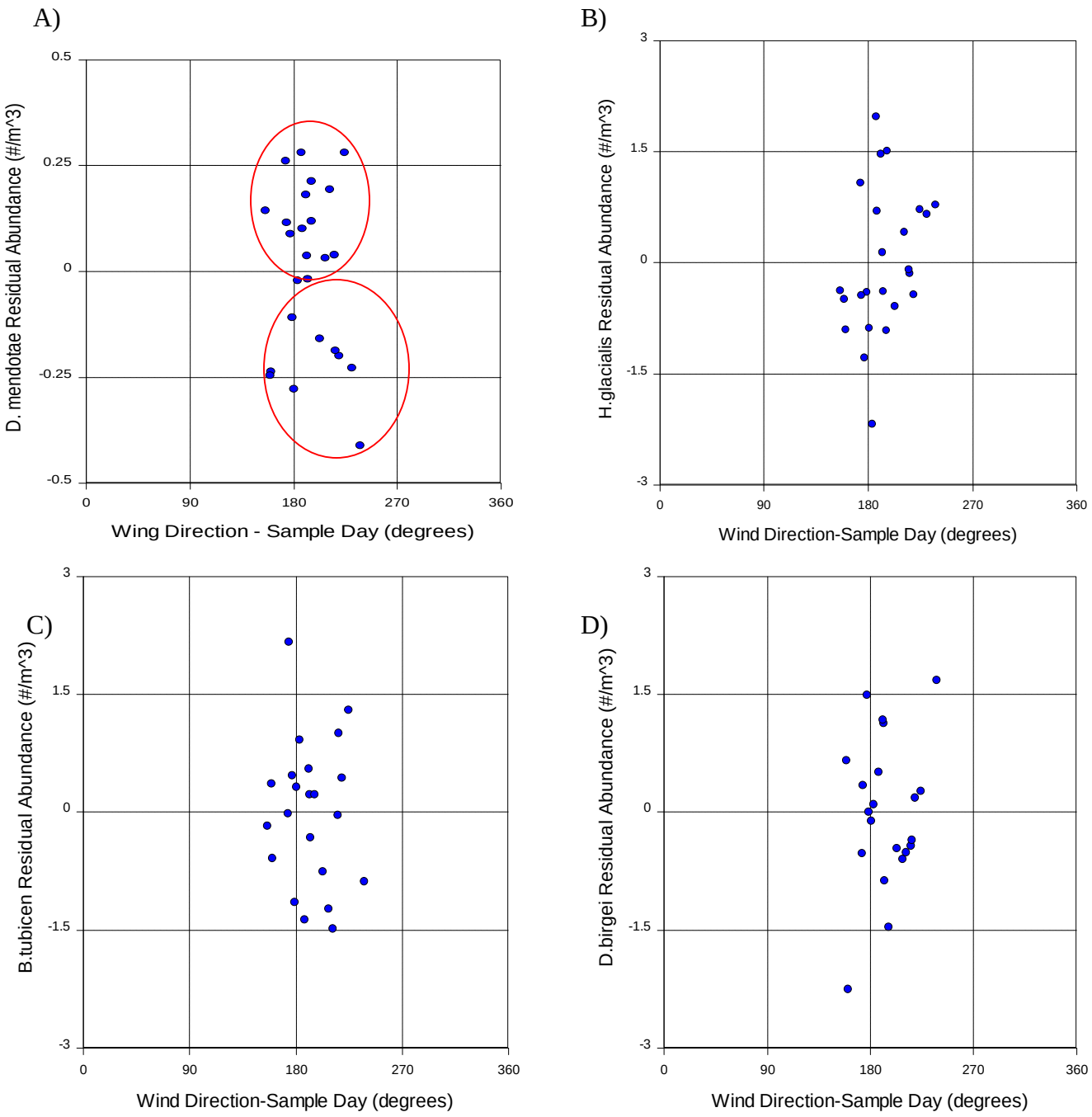


Figure 4.2a: Two-Sample scatterplot depicting the distribution the residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. A-D: *D.mendotae, H.glacialis, B.tubicen,* and *D.birgei*. Each dot denotes a particular yearly average. Plots were generated using Oriana 3.0. The bivariate linear-circular association measure, r^2, which relates to this plot, determines the significance of the association between the data present. The circles indicate the significant difference between the negative and positive residuals

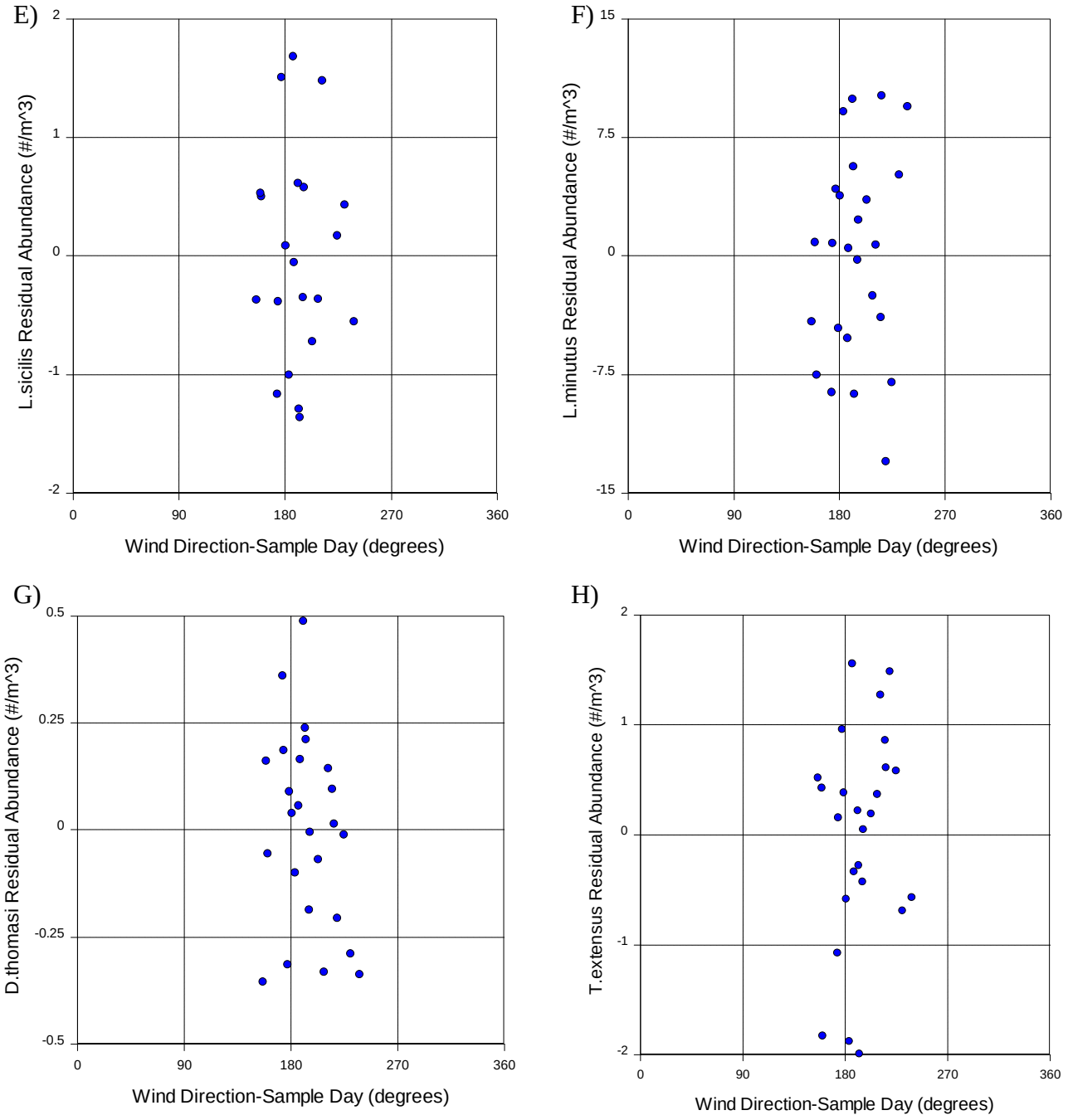


Figure 4.2b: Two-Sample scatterplot depicting the distribution the residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. E-H: *L.sicilis, Lminutus, D.thomasi* and *T.extensus*. Each dot denotes a particular yearly average. Plots were generated using Oriana 3.0. The bivariate linear-circular association measure, r^2, which relates to this plot, determines the significance of the association between the data present.

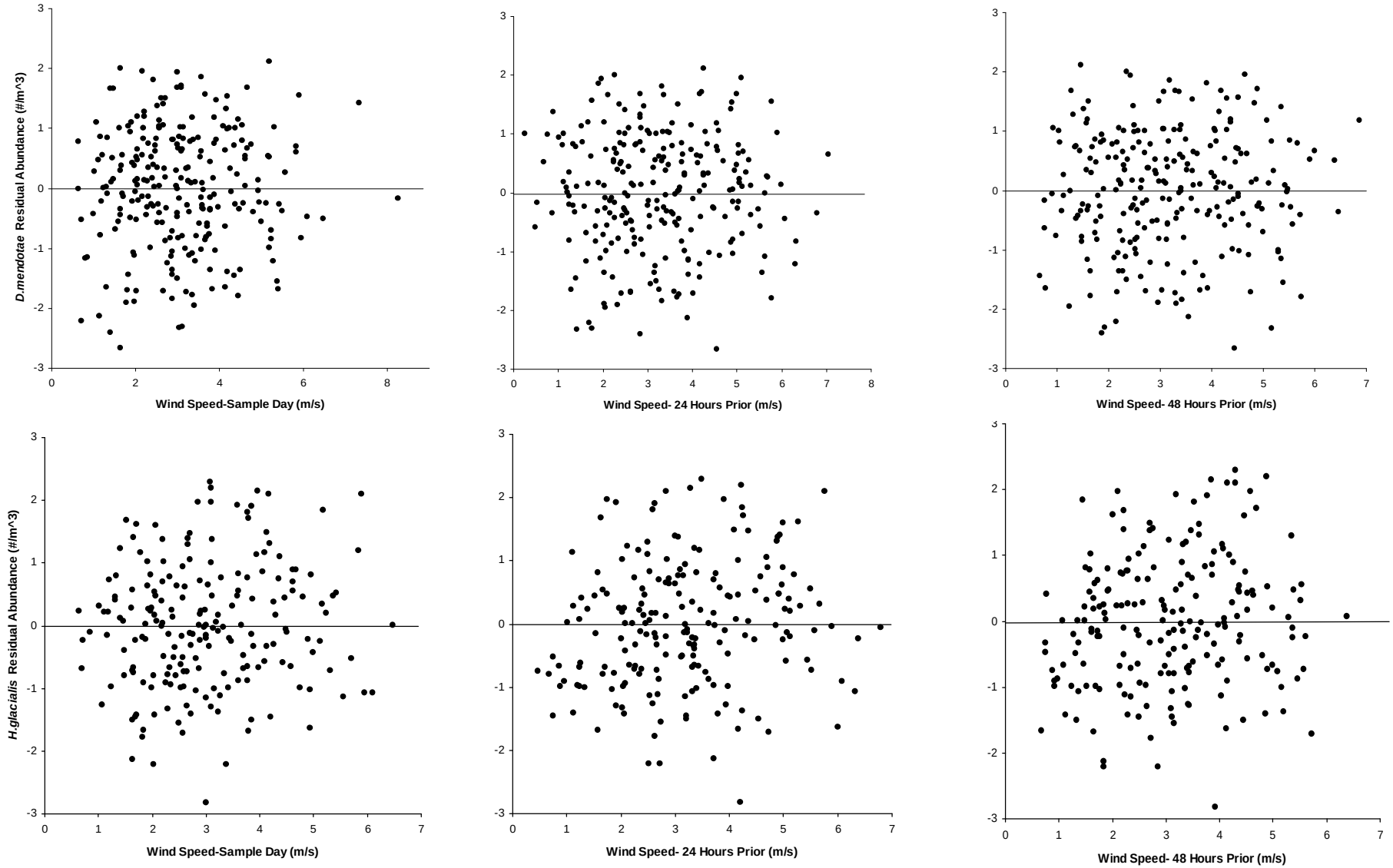
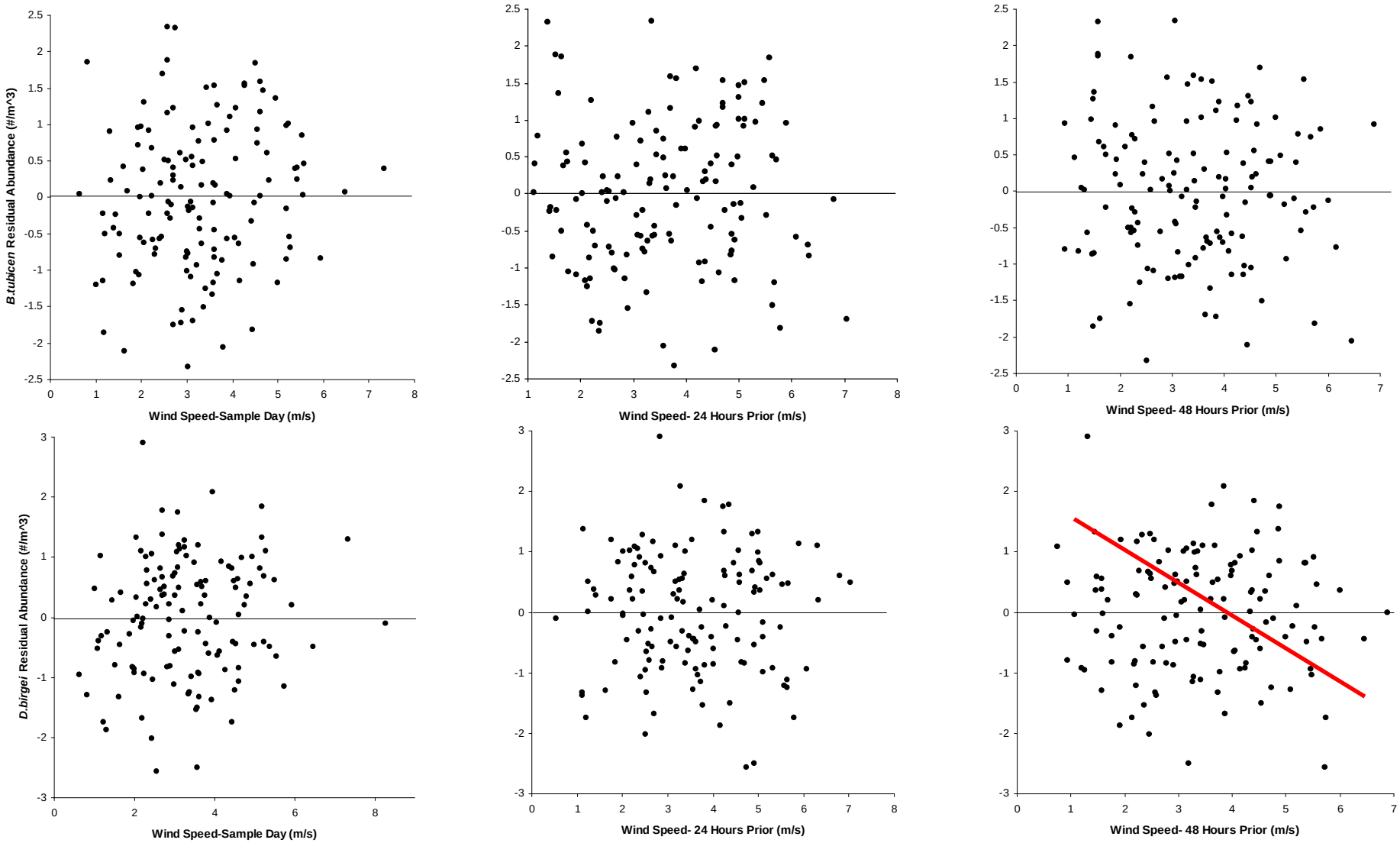
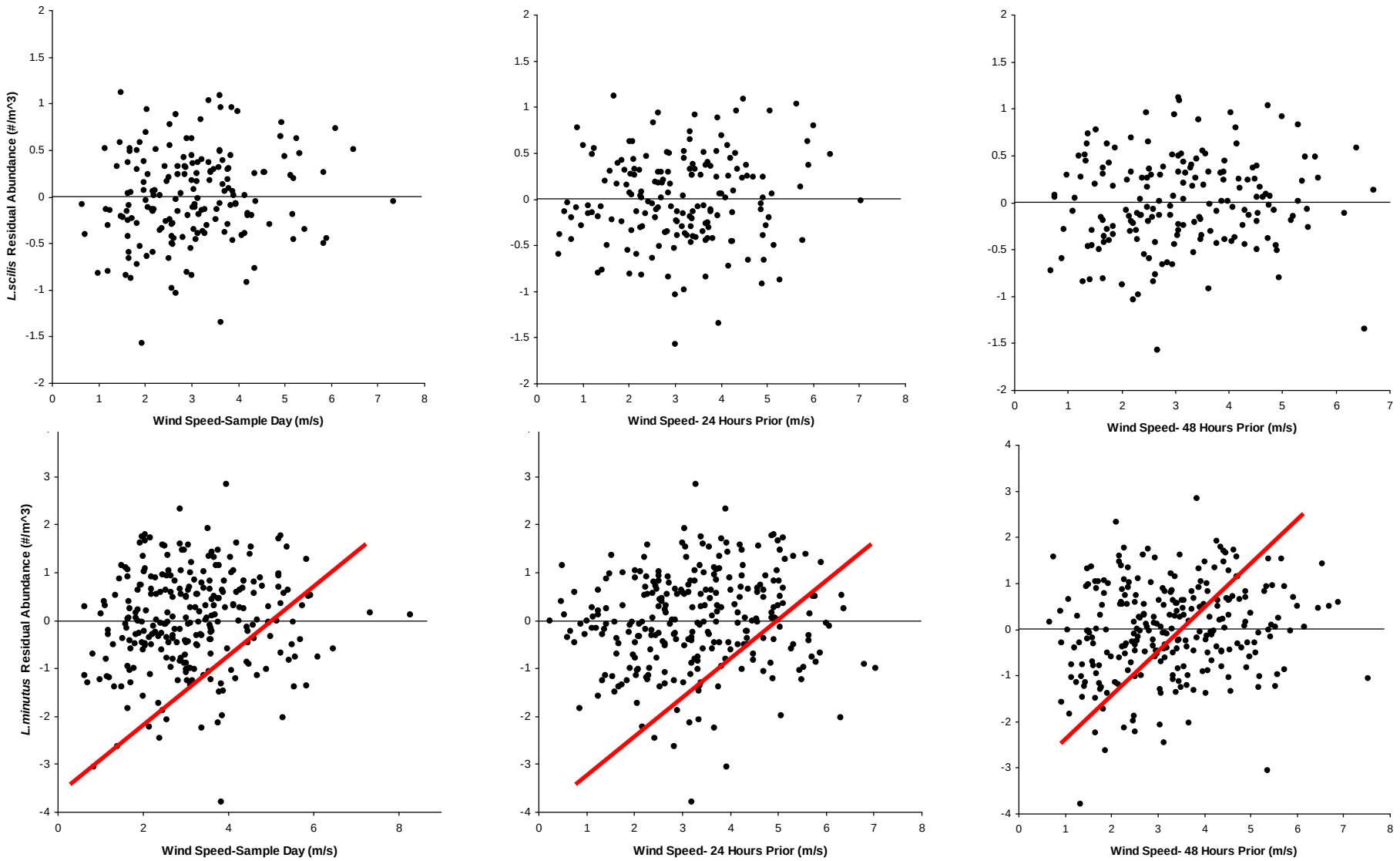


Figure 4.3a: Scatterplots depicting the daily residual abundance of the chosen zooplankton and the wind speed over Muskoka Airport, Ontario during 1980-2004. Residual abundance was generated after correcting for year/day of year.



Fgure 4.3b: Scatterplots depicting the daily residual abundance of the chosen zooplankton species and the wind speed over Muskoka Airport, Ontario during 1980-2004. Residual abundance was generated after correcting for year/day of year. The line indicates the significant trend.



Figue.3c: Scatterplots depicting the daily residual abundance of the chosen zooplankton species and the wind speed over Muskoka Airport, Ontario during 1980-2004. Residual abundance was generated after correcting for year/day of year. The line indicates the significant trend.

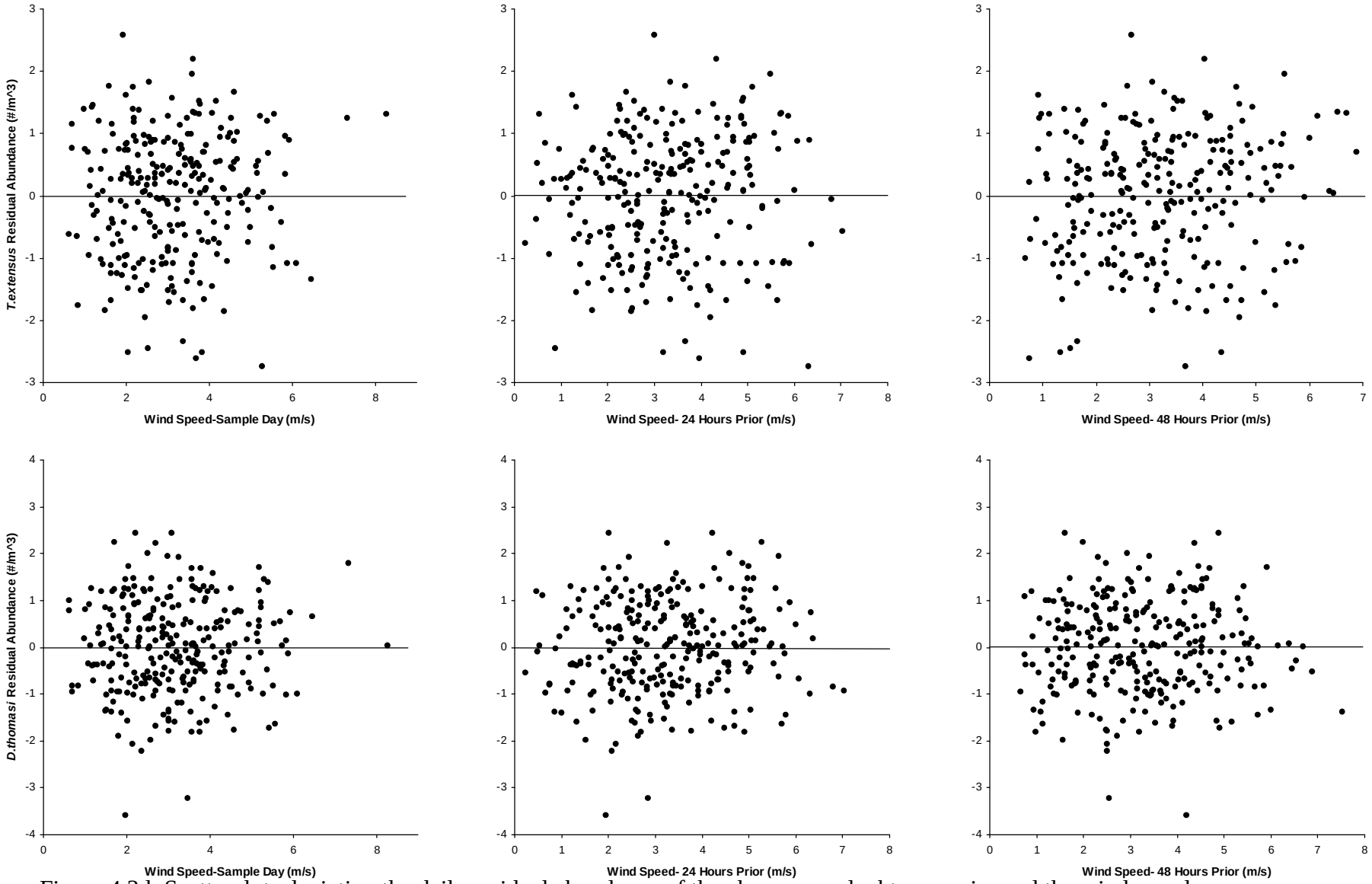


Figure 4.3d: Scatterplots depicting the daily residual abundance of the chosen zooplankton species and the wind speed over Muskoka Airport, Ontario during 1980-2004. Residual abundance was generated after correcting for year/day of year.

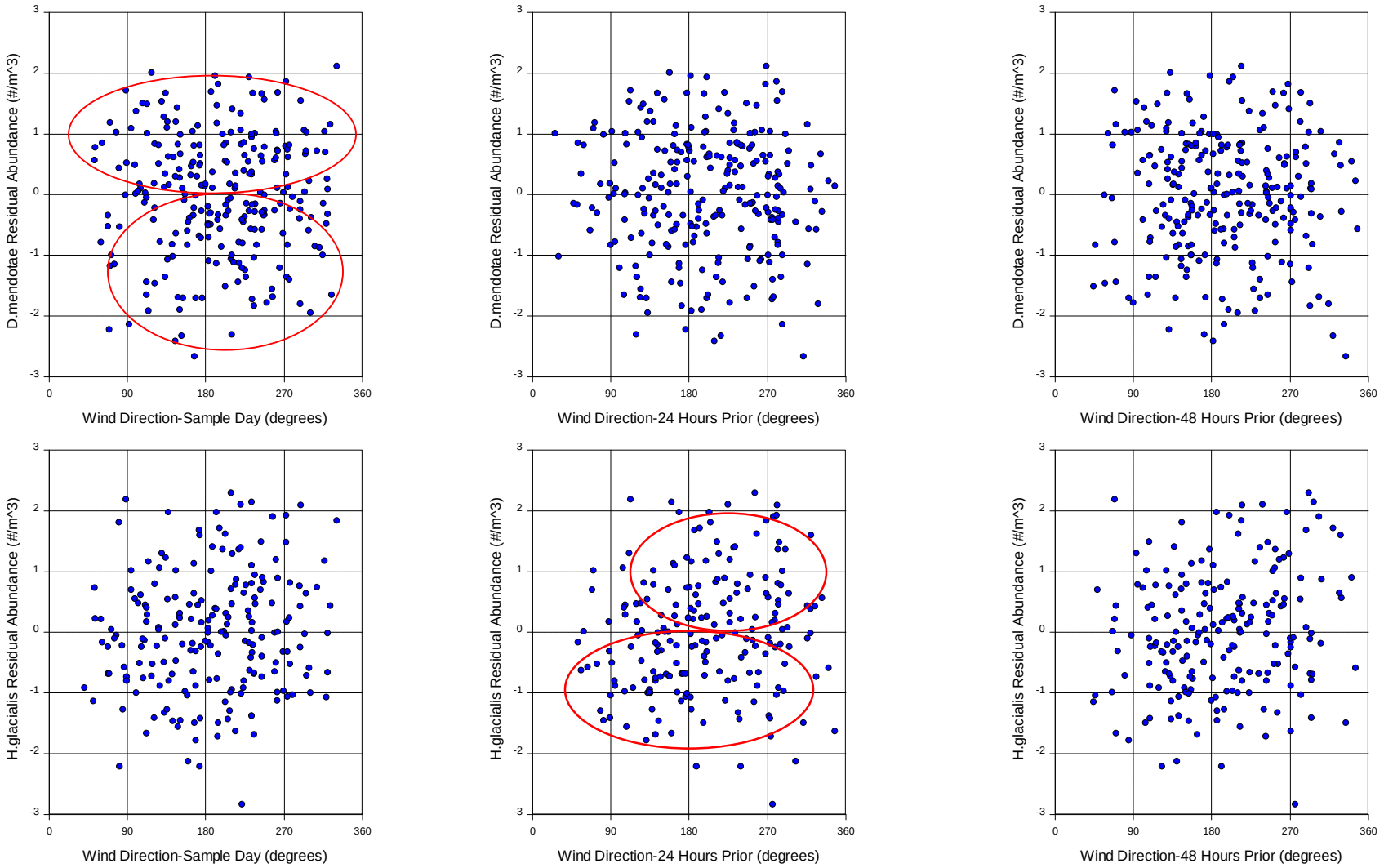


Figure 4.4a: Two-Sample scatterplot depicting the distribution of the daily residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. Residual abundance was generated after correcting for year/day of year. Plots were generated using Oriana 4.0. Circles indicate where there is significant deviation.

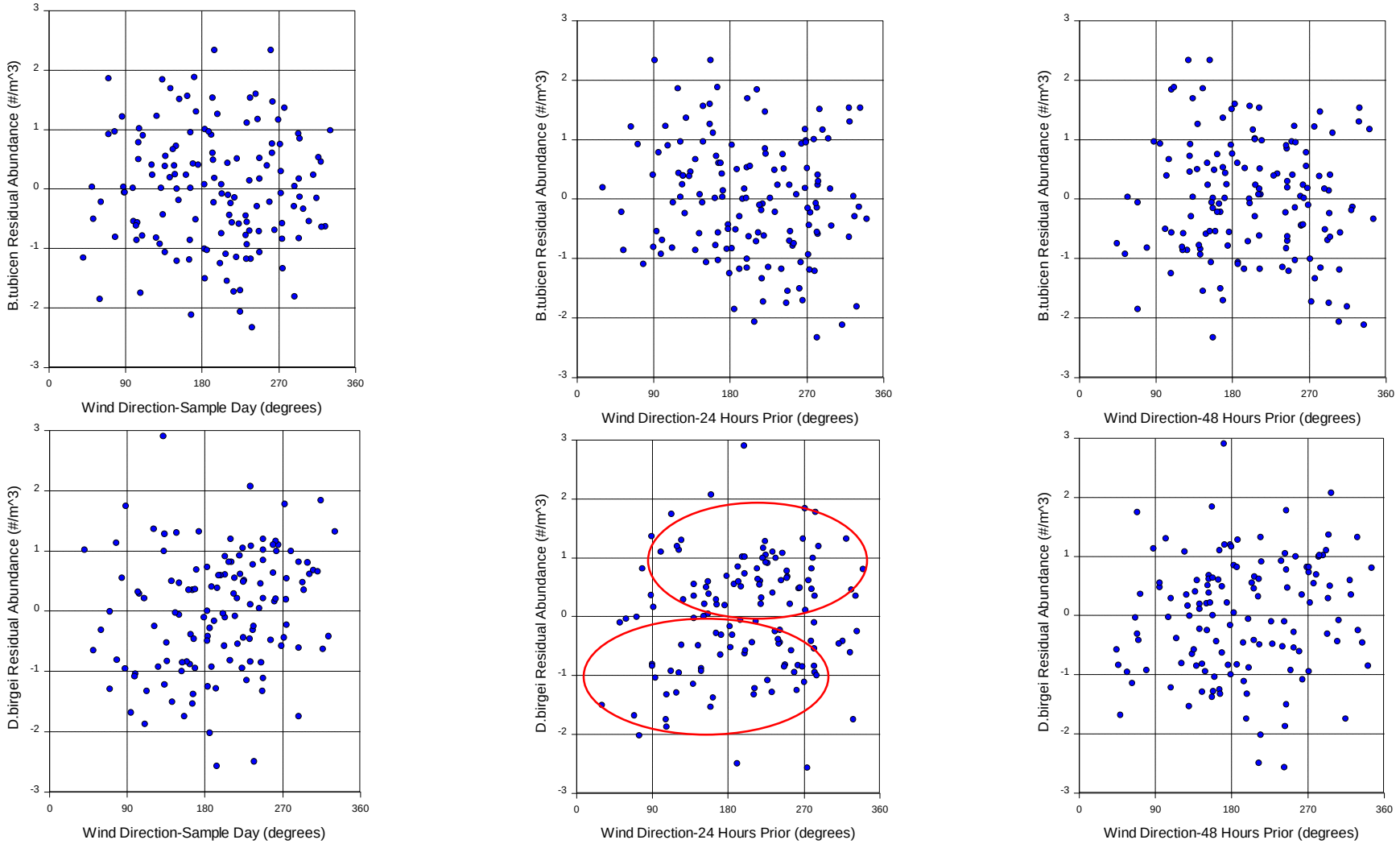


Figure 4.4b: Two-Sample scatterplot depicting the distribution of the daily residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. Residual abundance was generated after correcting for year/day of year. Plots were generated using Oriana 4.0. Circles indicate where there is significant deviation.

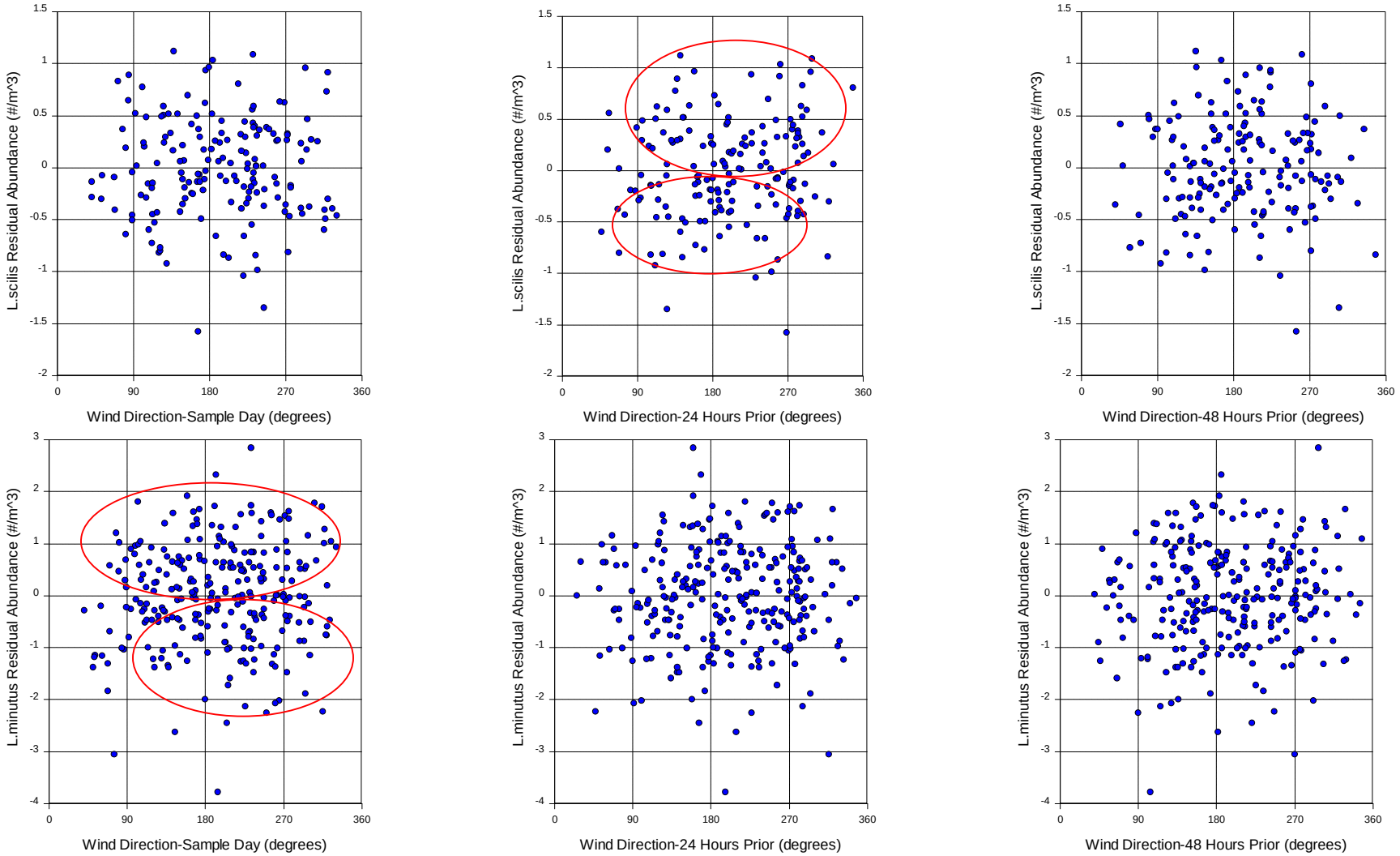


Figure 4.4c: Two-Sample scatterplot depicting the distribution of the daily residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. Residual abundance was generated after correcting for year/day of year. Plots were generated using Oriana 4.0. Circles indicate where there is significant deviation.

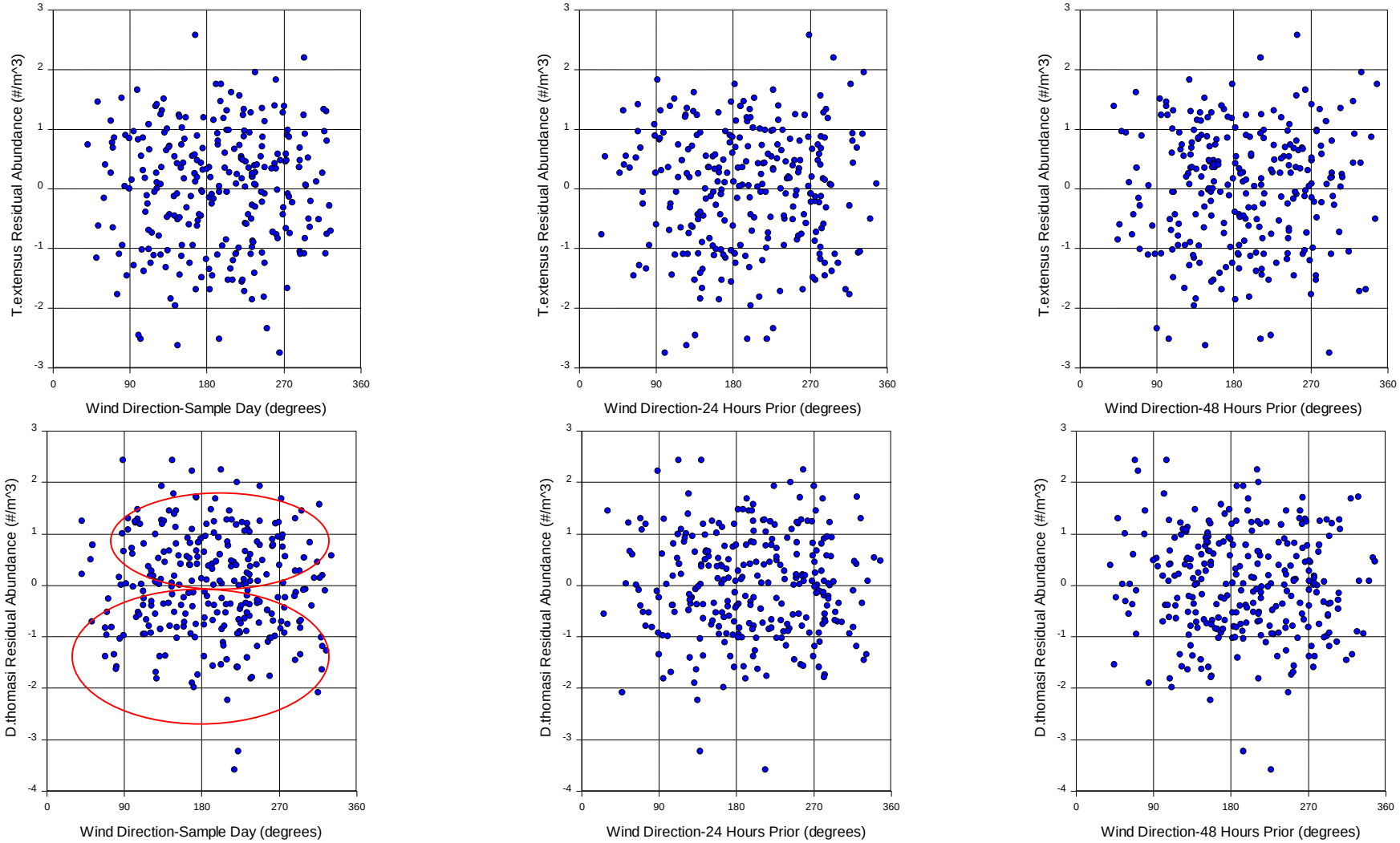


Figure 4.4d: Two-Sample scatterplot depicting the distribution of the daily residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. Residual abundance was generated after correcting for year/day of year. Plots were generated using Oriana 4.0. Circles indicate where there is significant deviation.

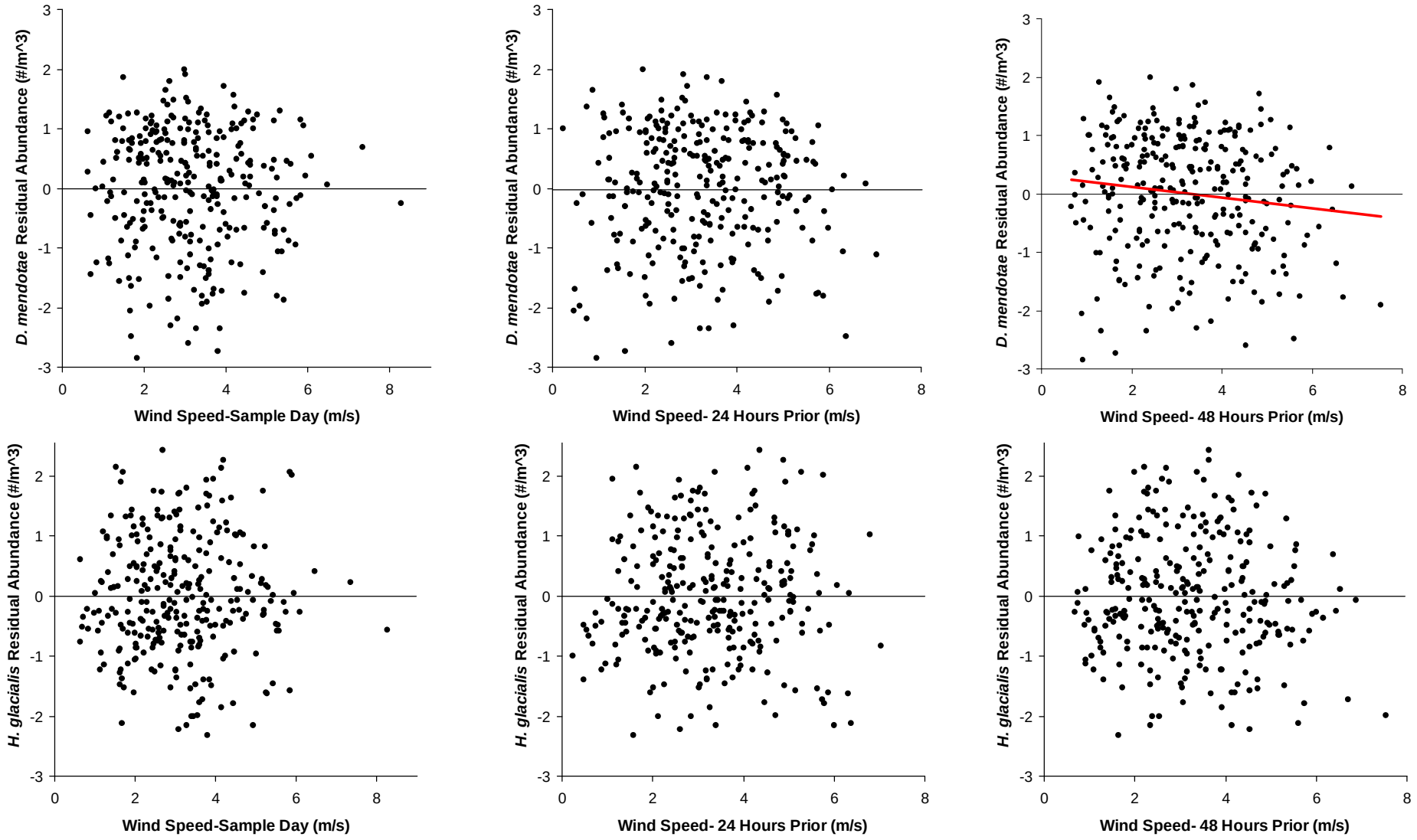


Figure 4.5a: Scatterplots depicting the daily residual abundance of the chosen zooplankton and the wind speed over Muskoka Airport, Ontario during 1980-2004. Residual abundance was generated after correcting for year/day of year and chemistry combined. The line indicates the significant trend.

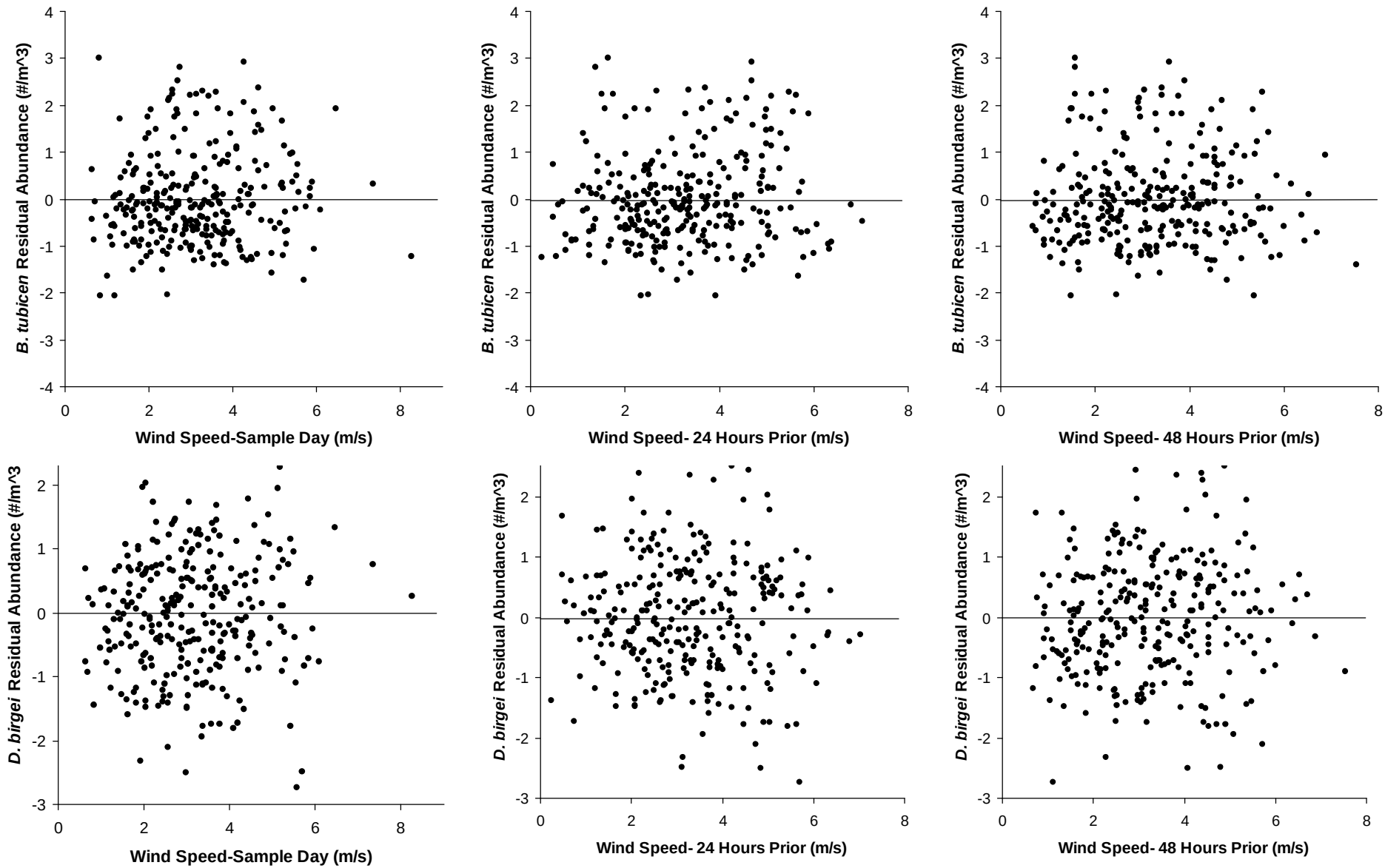


Figure 4.5b: Scatterplots depicting the daily residual abundance of the chosen zooplankton and wind speed over Muskoka Airport during 1980-2004. Residual abundance was generated after correcting for year/day of year and chemistry combined.

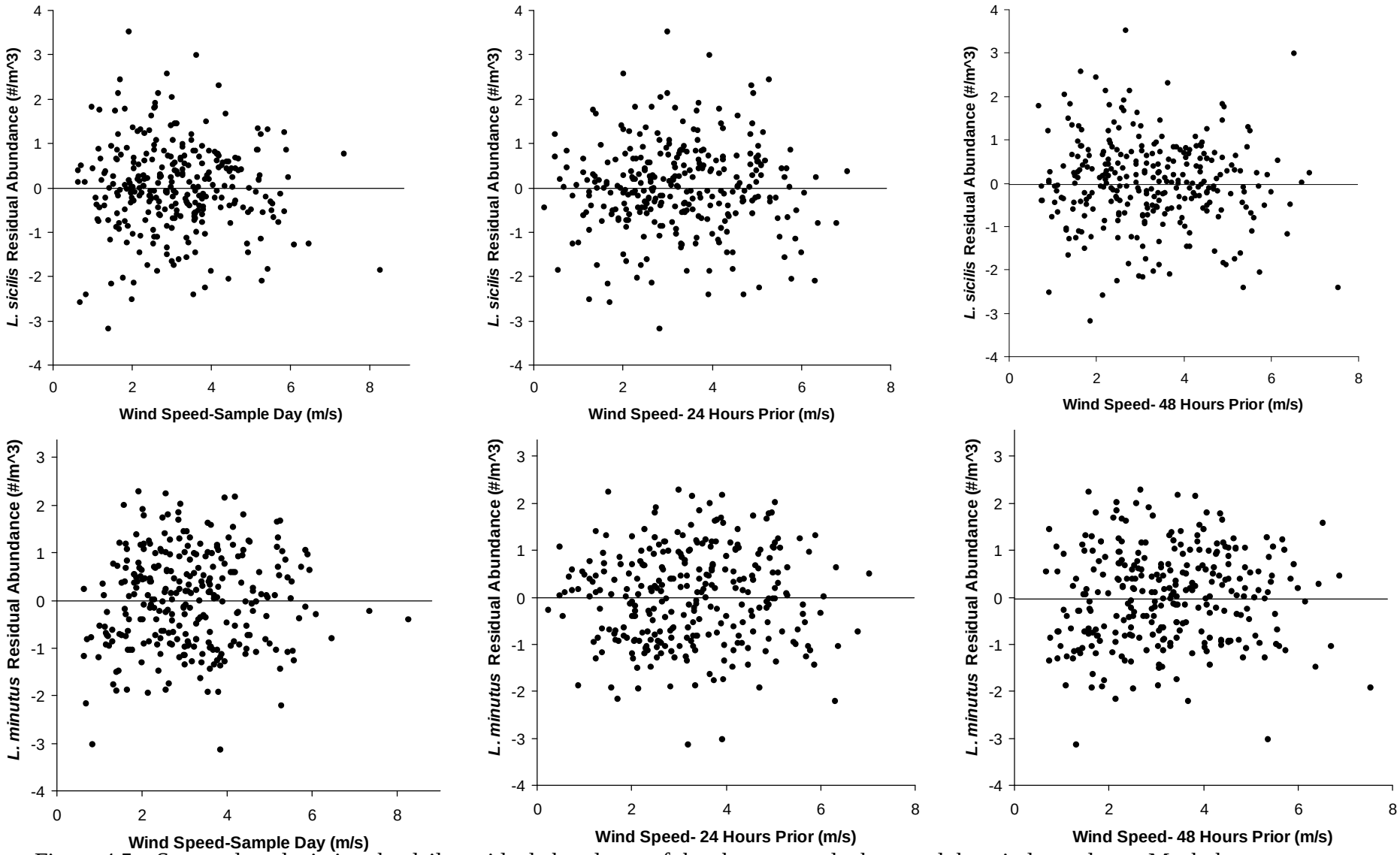


Figure 4.5c: Scatterplots depicting the daily residual abundance of the chosen zooplankton and the wind speed over Muskoka Airport during 1980-2004. Residual abundance was generated after correcting for year/day of year and chemistry combined.

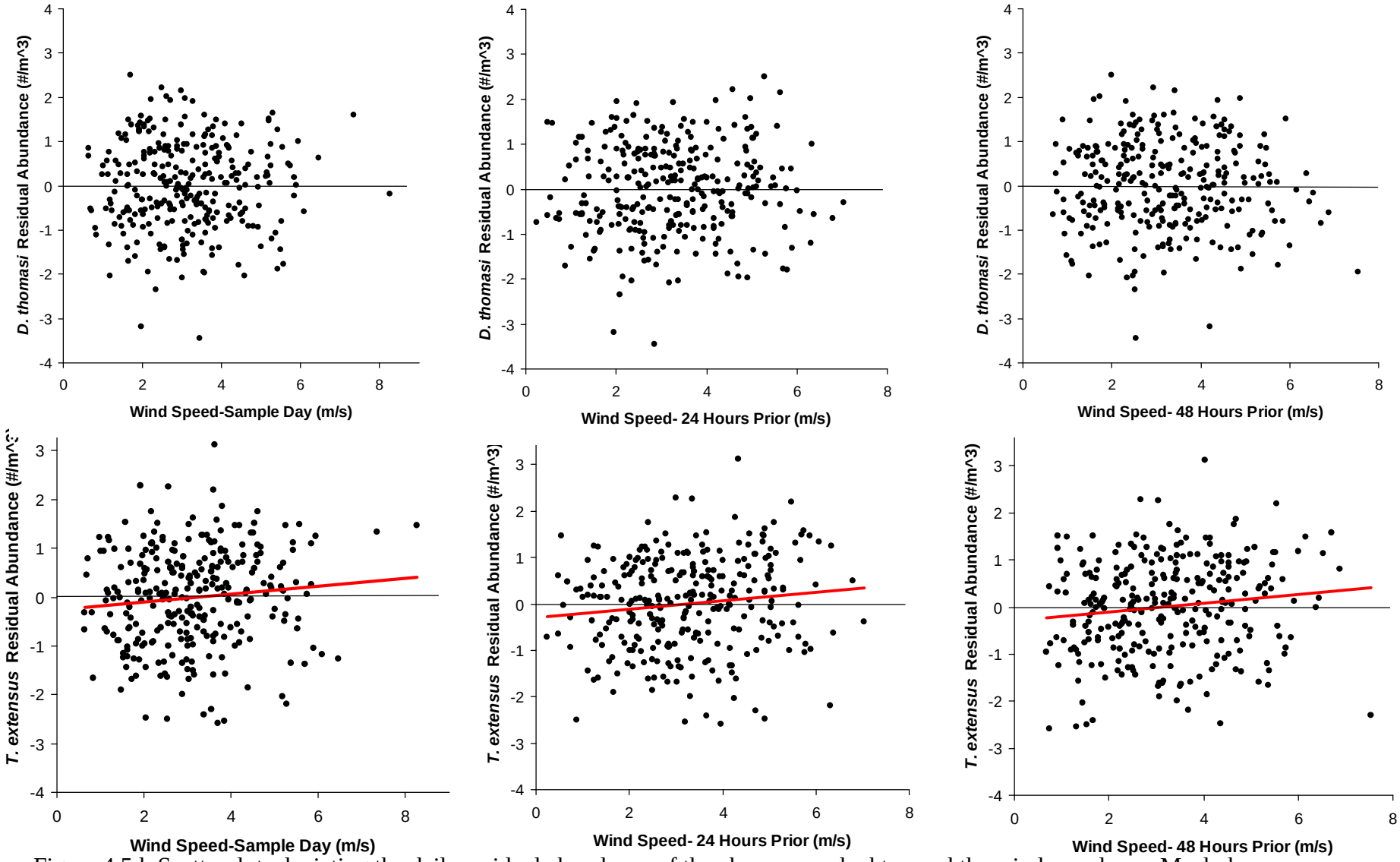


Figure 4.5d: Scatterplots depicting the daily residual abundance of the chosen zooplankton and the wind speed over Muskoka Airport, Ontario during 1980-2004. Residual abundance was generated after correcting for year/day of year and chemistry combined. The thick line indicates the significant trend.

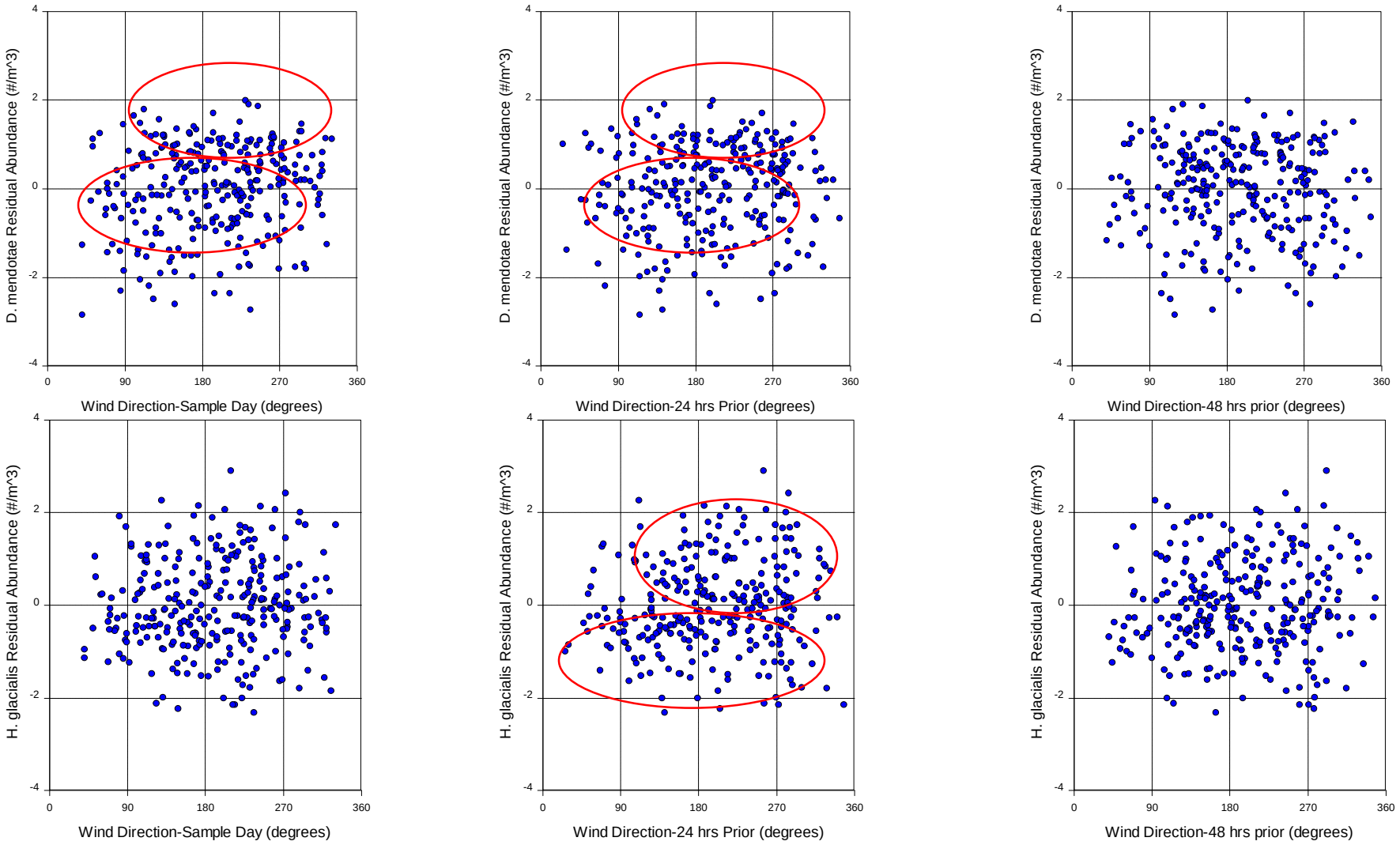


Figure 4.6a: Two-Sample scatterplot depicting the distribution of the daily residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. Residual abundance was generated after correcting for year/day of year and chemistry combined. Plots were generated using Oriana 4.0. The circles indicate areas where there is significant deviation.

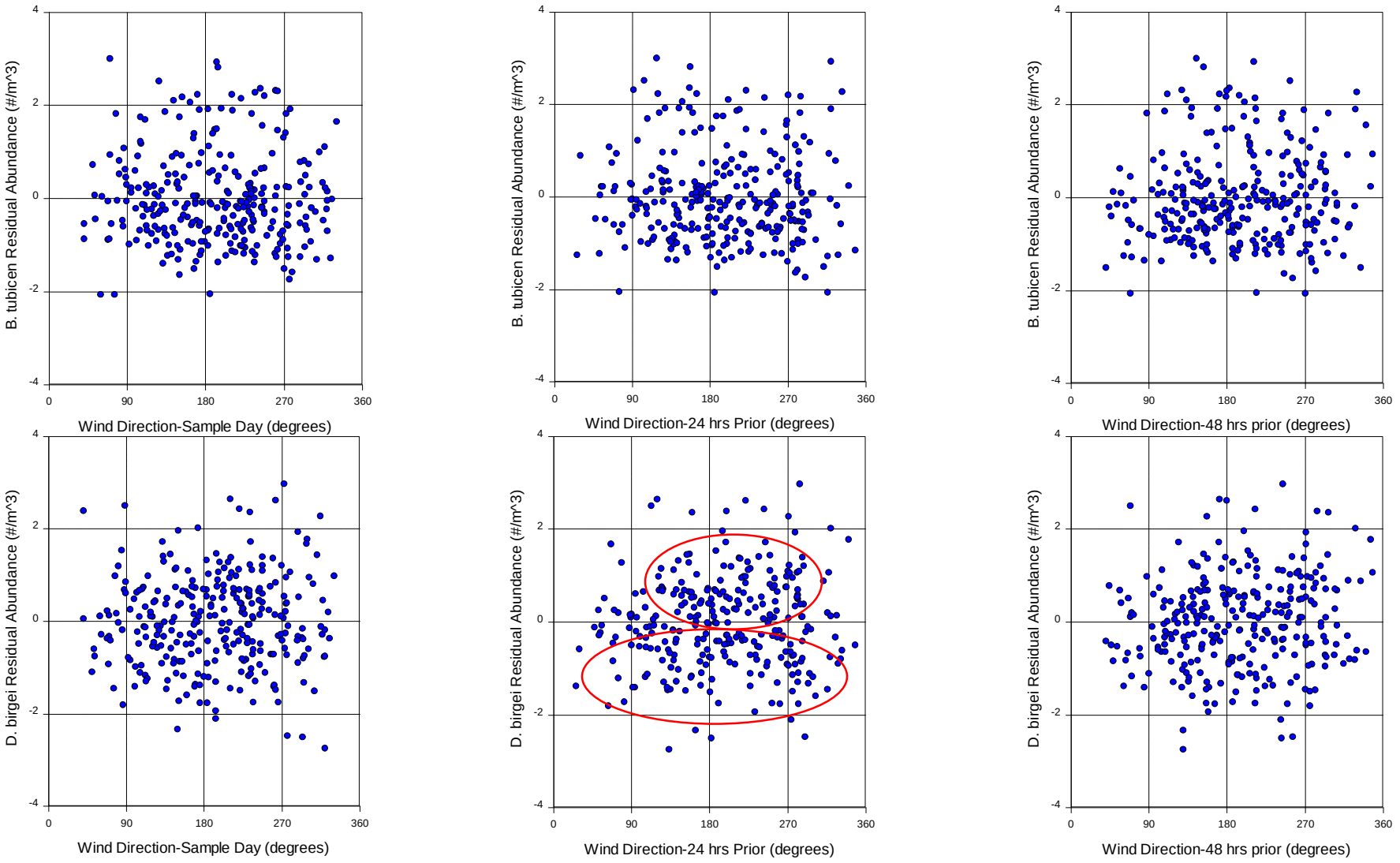


Figure 4.6b: Two-Sample scatterplot depicting the distribution of the daily residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. Residual abundance was generated after correcting for year/day of year and chemistry combined. Plots were generated using Oriana 4.0. The circles indicate areas where there is significant deviation.

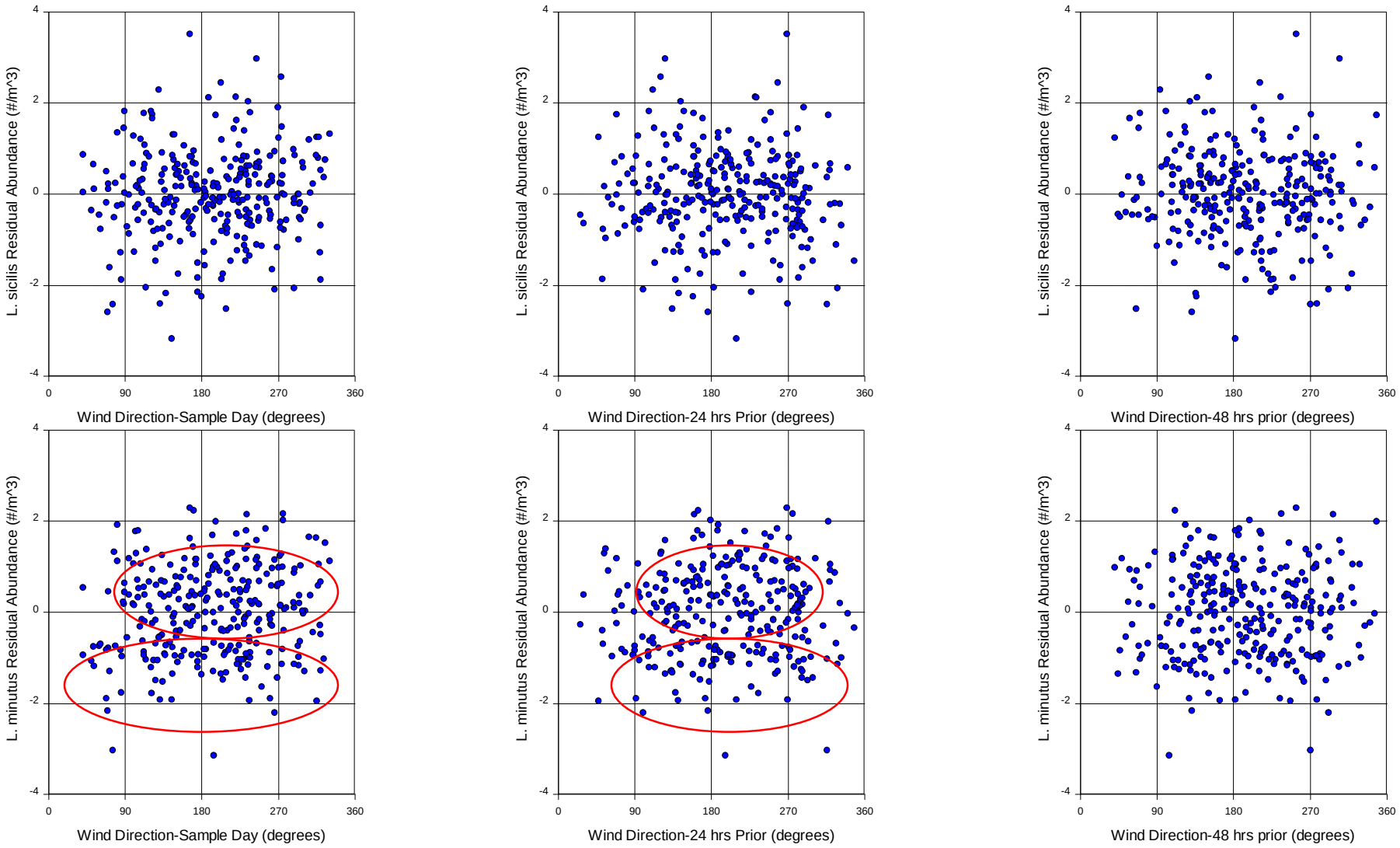


Figure 4.6c: Two-Sample scatterplot depicting the distribution of the daily residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. Residual abundance was generated after correcting for year/day of year and chemistry combined. Plots were generated using Oriana 4.0. The circles indicate areas where there is significant deviation.

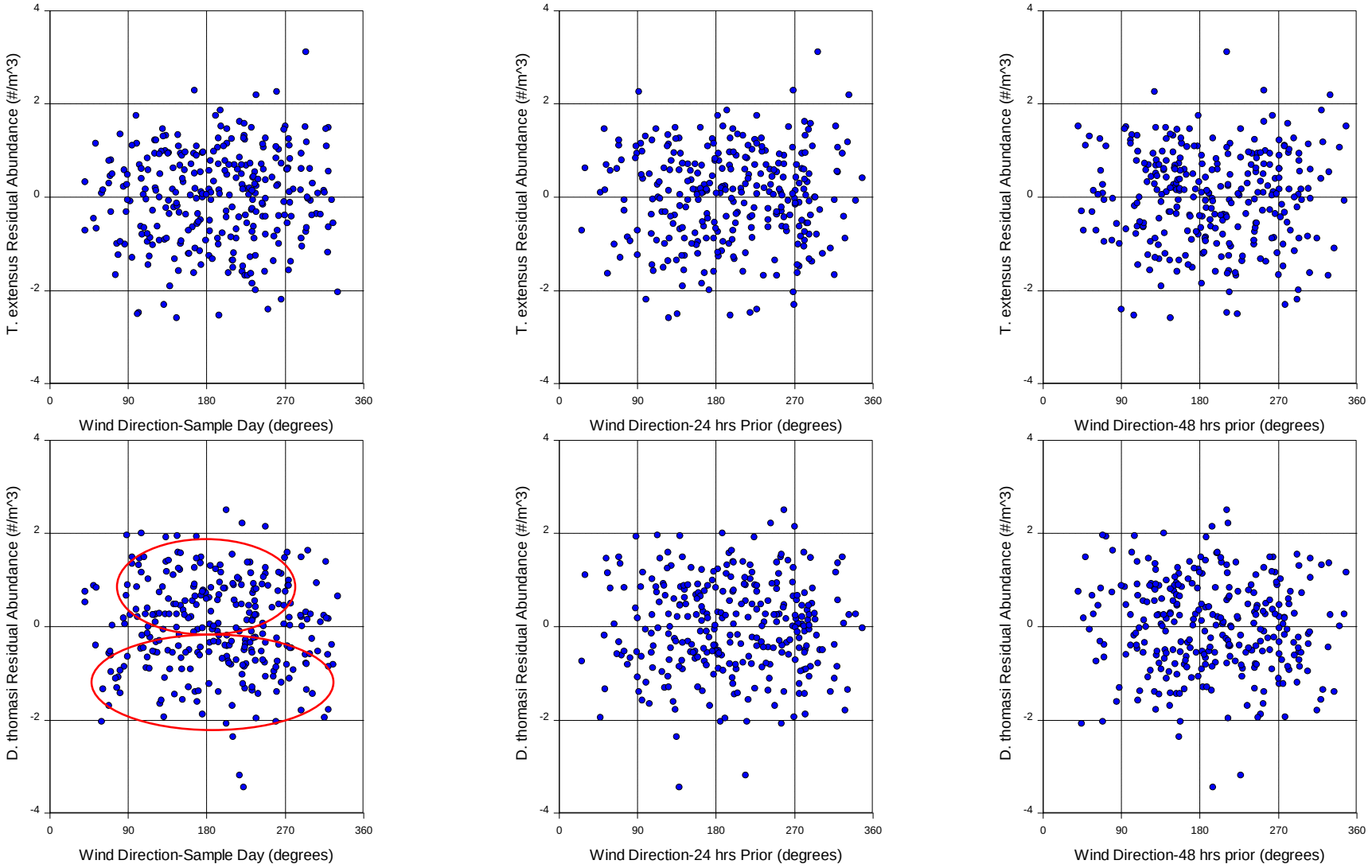


Figure 4.6d: Two-Sample scatterplot depicting the distribution of the daily residual abundance with respect to a particular wind direction for each zooplankton species between 1980-2004 from Harp Lake, Ontario. Residual abundance was generated after correcting for year/day of year and chemistry combined. Plots were generated using Oriana 4.0. The circles indicate areas where there is significant deviation.